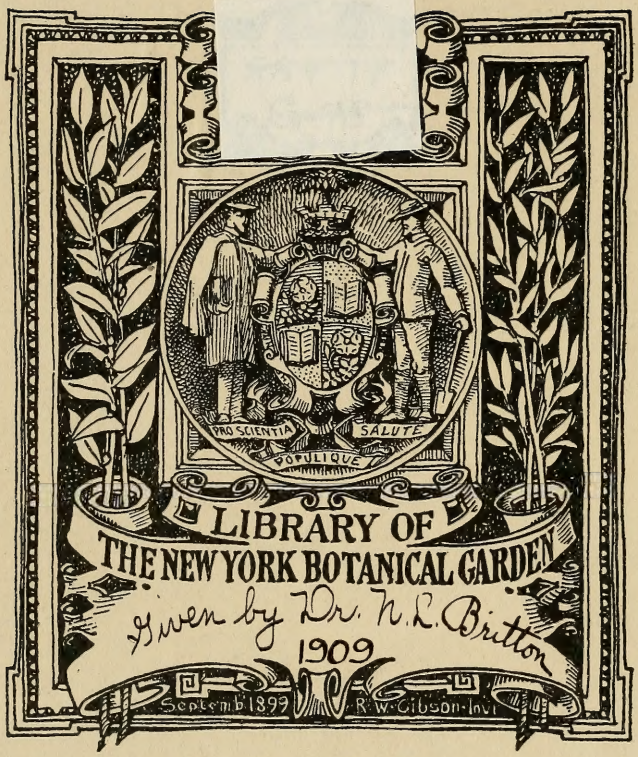
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VOLUME 14, PAGES 59-170 DECEMBER, 1908

The Morphology of Ruppia Maritima

BY

ARTHUR HARMOUNT GRAVES, Ph.D.
INSTRUCTOR IN BOTANY IN YALE UNIVERSITY

PUBLISHED UNDER THE AUSPICES OF
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INTRODUCTION

Of late years there has been manifested a tendency toward a systematic investigation of the internal structure of plant species, as contrasted with the more superficial description of external characters by systematists. For although, as stated by Campbell (1897), a description of external characters "is usually quite sufficient for the mere identification of a plant, and for determining its relation to nearly allied forms, it is quite inadequate for settling questions of relationship between more remote groups, and especially those of obscure affinities."

This movement has been directed especially to the study of the origin and development of the sexual generation in Spermatophytes and the problems of embryology in this group, resulting in an overwhelming mass of literature on these subjects.

But, in the meantime, it is commendable that some botanists have also directed their attention to a study of the internal structure of the vegetative organs; for it is only by a complete account of the development and structure of the whole plant, together with its life history, that we can hope to acquire sufficient knowledge for the solution of one of the most interesting and vitally important problems in all plant morphology—i. e., the interrelationship of the various plant groups.

Some of the recent works of Campbell (1897, 1898) are most noteworthy in presenting in this way a connected account of several species, especially certain little understood monocotyledons.

The present work, extending over a period of five years, was undertaken with a similar purpose; and seeks to comprehend, as far as possible, a connected account of the development and structure of the plant organs, together with the life history, of one of the simpler monocotyledons, *Ruppia maritima*.

The Potamogetonaceae of Ascherson (1889) to which the genus Ruppia belongs, comprise an interesting family of remarkably simple plants. As to whether this simple structure represents a primitive or a reduced condition is an extremely important question, but in the present state of our knowledge a clear, unassailable verdict on either side is impossible. A discussion of this point will, however, be postponed for the present.

A few remarks may be in order here as to the literature which relates to the subject of this paper, and which I have found most helpful in its preparation. Ascherson (1889), in Engler and Prantl's Natürliche Pflanzenfamilien, cites the most important references bearing on the Potamogetonaceae up to the date of his contribution. Among these, the papers on Althenia by Prillieux (1864), Cymodocea by Bornet (1864), and Zostera by Grönland (1851) are valuable for their contributions to the morphology of these allied plants. In this respect, also, the works of Irmisch (1851 and 1858) are remarkable for the accuracy with which they describe the external morphological relations of *R. rostellata* and other Potamogetonaceae. Of later works, which are especially useful in a comparative morphological study of the vegetative organs, are, among others, those of Sauvageau (1891, II), Campbell (1897) and Goebel (1898). As to ecological considerations pertaining to water plants, the work of Schenck (1886) deserves especial mention. In the preparation of the parts on the reproductive organs, embryo, &c., the works cited are too numerous to mention here, and the reader is referred to the bibliography (p. 165).

If we except a rather doubtful reference of Hofmeister, (1861, Figures 1–7, Pl. II, and see p. 148 of this paper), the only investigation of *Ruppia maritima* which has ever been published, so far as I can ascertain, is that of Roze (1894), who describes chiefly the conditions of fertilization, but also presents a valuable historical review of the whole genus. Others, it is true, such as Miss Scott (1906) and Chrysler (1907), have dealt with special features of the plant, in the course of their comparative morphological investigations.

Ruppia rostellata, on the other hand, if we piece together the results of various observers, has been pretty thoroughly worked out. First Irmisch (1851 and 1858) described carefully its external morphological characters; next, Wille (1883) studied the development of the embryo, and quite recently Murbeck (1902) published an admirable paper on the reproductive organs and embryo.

The genus Ruppia is aquatic, characterized by its long, linear, grass-like leaves with basal sheaths, and grows in brackish and salt water (but probably never salt water of normal ocean strength, see p. 124), in creeks and bays along the coast and in the neighborhood of inland salt springs, throughout all parts of the temperate and tropical zones. Except at low tide it is completely submerged until the period of flowering, when it produces its flowers a short distance (1–3 cm.) above the surface of the water. The flowers, always two to each peduncle, are borne one above the other, on

opposite sides of the rhachis, the latter being homologous to a spadix, but not at all fleshy. The flowers are naked and consist of two practically sessile anthers, each with its two large sacs or thecae separate and arranged transversely on the rhachis, making a diamond-shaped arrangement, in the center of which is a group of pistils, always four in number in the specimens I have examined (Pl. IX, fig. 49).[1] After the shedding of the pollen, the pistils if fertilized develop a stipe or pedicel of considerable length (Pl. IV, fig. 13). The peduncle, or floral axis, however, elongates whether fertilization is consummated or not. After fertilization the fruit is drawn below the surface of the water, the elongated peduncle usually coiling up to aid in this process (see p. 85).

In company with most of the submerged plants, Ruppia is perennial. The majority of the leaves and stems die at the approach of cold weather, leaving the living rootstock buried in the mud. Some green leaves, however, remain, connected with the rootstock, and lie at the bottom of the ditch or pool, so that it is possible to collect all of the vegetative organs all winter.

One locality, indeed, is worthy of note, where *Ruppia maritima* flourishes all winter. Here, possibly on account of springs, the water is tempered somewhat, and I have gathered Ruppia in a green, vigorous condition, when the surface of the ditch was covered with ice over an inch in thickness. Although there are doubtless springs here, the water nevertheless contains a large percentage of salt. It is quite possible that there are many other similar locations where Ruppia grows all through the winter.

In no case, however, have I found the bulbous winter buds, which have been noted in the Potamogetons by Irmisch (1858).

As indicated by Britton and Brown (1896 vol. I, p. 79), considerable variation exists in *Ruppia maritima.* Thus, one form which I have noticed especially, is of a more slender habit, with narrower leaves and stems than those of the ordinary individual. Its branching is ultimately quite irregular, although the system accords with that of the normal form. This form grows in quiet pools.

There is, moreover, still considerable uncertainty as to the number of existing species of Ruppia (Ascherson, 1889; Saüvageau, 1891, II, p. 209; Roze, 1894, p. 479). The question is such a large one that it cannot be discussed here, and would require, besides, a careful study of herbarium material from different parts of the world. I will only state that as far as I can learn from a study of systematic

[1] But see Roze, 1894, p. 479.

descriptions and figures (Griffith, 1851, I–II; Irmisch, 1858; Hillebrand, 1888; Ascherson, 1889; Sauvageau, 1891, II; Hooker, 1894; Roze, 1894; Britton, 1907), four species may be safely recognized; namely, *R. maritima* L., *R. rostellata* Koch, *R. brachypus* Gay, and *R. occidentalis* Wats.

All of the material for the present work was collected in tidal ditches in Fort Hale Park, near New Haven, Conn. Here it grows in abundance, forming large tufts with its grass-like leaves, which follow easily the direction of the current. At extreme low tide a large portion of the plant floats, but at high tide it is completely submerged. The period of flowering commences in June and continues until the severe frosts in autumn, up to which time, even in October, I have gathered flowers in good condition.

The material was killed either in chromacetic acid, Flemming's solution, or Keyser's fluid. The first seemed the best, although the others gave good results. Several stains were used: for general work haematoxylin and erythrosin; for cytological study in the development of the male and female gametophytes, &c., and the embryo, the triple stain was used with excellent results. For the latter investigations Heidenhain's iron haematoxylin was also found to be good. In all, about 20,000 microtome sections were cut of the different parts of the plant. For all of the microtechnique Chamberlain's "Methods in Plant Histology" was found invaluable, and in all preparations the directions given therein were closely followed.

I would like to avail myself of this opportunity to express my gratitude to Professor Alexander W. Evans, Eaton Professor of Botany in Yale University, for the great interest he has taken in the work and for the invaluable criticism and suggestions which he has been ever ready to give. I desire also to thank Professor W. R. Coe, Professor J. W. Toumey, and Dr. A. L. Dean, of Yale University, for their kindness in offering suggestions, material, &c.

THE MORPHOLOGY OF THE VEGETATIVE ORGANS

Stem

A. General Characters

Under the heading of "Stem" may be classed several parts of the plant, all of which are cauline in their morphology and origin, but differ to some extent in their functions and relations to the other parts of the plant. The horizontal axis, which lies prostrate on the soil, bearing the roots and upright shoots, may be termed the *rootstock*;[1] the axis of the upright shoot may for convenience be designated the *stem*; the parts which bear the flowers and fruit we may speak of respectively as *peduncle*, *rhachis*, and *stipe*.

In general, all these parts are slender, terete, and of a whitish color, although the stem at times assumes a greenish tinge due to a small content of chlorophyll.

I shall consider first the branching and anatomy of the stem and rootstock; next, the development of the stem structures which are connected with the production of flowers and fruit, comparing their anatomy with that of the first two structures.

B. Branching

1. Branching in *Ruppia maritima*.

Two principal systems of branching occur in Ruppia: one in stem and rootstock and connected with the ordinary growth, which we may call the vegetative branch system; and the other in the stem only, and associated with the production of flowers, which we may therefore designate the inflorescent branch system.

a. Vegetative Branch System.

The vegetative branch system is a distichous monopodium, the branches being borne alternately on opposite sides of the axis and in the same plane. In the rootstock, indeed, except near its growing point, this initial arrangement is generally later much obscured, due to the upward growth of many of the lateral branches (Pl. VII,

[1] As will readily be seen—a point which will be brought out more clearly later (p. 82)—the rootstock does not differ from the stem from a morphological point of view, either externally or internally; for any stem, by becoming horizontal and producing roots at the nodes, assumes the character of what I have termed the rootstock.

fig. 36). In the case of the stem, however, the natural arrangement often remains apparent (Pl. I, fig. 2; Pl. II, fig. 6).

On account of this distichous system, it is possible to cut a longitudinal section through all of the branches and the stem at the same time, especially if the region of the growing point is selected, as is represented in Pl. I, fig. 1 (cf. Pl. VI, fig. 25).

A study of this figure of a vigorously developing stem apex will show clearly the order of development and the orientation of the branches. Since the origin of the branches is inseparably connected with the leaf development, it will be necessary to include in a description of the figure some reference to leaf development.

The apical growing point $G\,P$ has given off in alternate succession the primary leaves L^{I}, L^{II}, L^{III}, L^{IV}, &c. A secondary growing point arises in the axil of each of these leaves, which develops leaves in the same manner. The first leaf, however, is a scale leaf, which will be discussed at length later. (See p. 99.)

Since L^{I}, L^{II}, L^{III}, L^{IV}, &c. are developed in acropetal succession and hence show equal gradations in age, a study of their successive axillary structures presents a clear idea of the manner of development of the branch. The youngest leaves, L^{VIII} and L^{VII} are hardly more than protuberances from opposite sides of the growing point, and as yet reveal no structures in their axils. At L^{VI} we first see a small axillary growing point—the beginning of a branch. In the axil of L^{V} the rudimentary scale leaf, $v\,s\,l$, appears on the left of the growing point $g\,p^{(V)}$. At the base of L^{IV} we find the scale leaf $(v\,s\,l)$ in its normal position, and also on the left of the growing point point the first vegetative leaf of the branch, $l_1^{(IV)}$. The axils of L^{III} and L^{II} show successively advanced stages until in L^{I} appear four leaves of the branch besides the scale leaf;—$l_1^{(I)}$, $l_2^{(I)}$, $l_3^{(I)}$ and $l_4^{(I)}$. Moreover in the axils of $l_1^{(I)}$ and $l_2^{(I)}$ appear young growing points to form branches of a second order.

Such a growing point under ordinary conditions will develop in a regular way for some time, the leaves and axillary shoots appearing in acropetal succession and the nodes of increasing length basipetally, according to their age. This stage is represented in Pl. I, fig. 2, a sketch from a living specimen.

Sooner or later, however, in the course of the development of the system, its regularity becomes more and more modified to suit environmental relations, a condition which is of course true of any branch system. Pl. II, fig. 6 is a drawing from nature of the upper portion of a plant whose vegetative branch system has undergone

considerable modification in this way. The period of blooming is at hand, and although no flowers have yet appeared, we find flower buds at the ends of the lateral branches as well as at the termination of the main shoot itself.

Some of the modifications here exhibited are the varying orientation of nodes and internodes—an arrangement evidently brought about to obtain the most advantageous light, space, &c.;—the irregularity in length of internodes, those at the base of the plant being not necessarily the longest; and the number of leaves borne on the branches previous to the development of flowers, for since the latter must bloom above the surface of the water, the lowest branches must necessarily be longer and hence bear more leaves.

In its development of flower buds, the case is a good illustration of the manner of change from the vegetative branching to the inflorescent type, as described below.

b. Inflorescent Branch System.

Irmisch (1851) has accurately described the inflorescent type of branching in *R. rostellata*, but for the sake of completeness and confirmation in *R. maritima*, I will review the more important points.

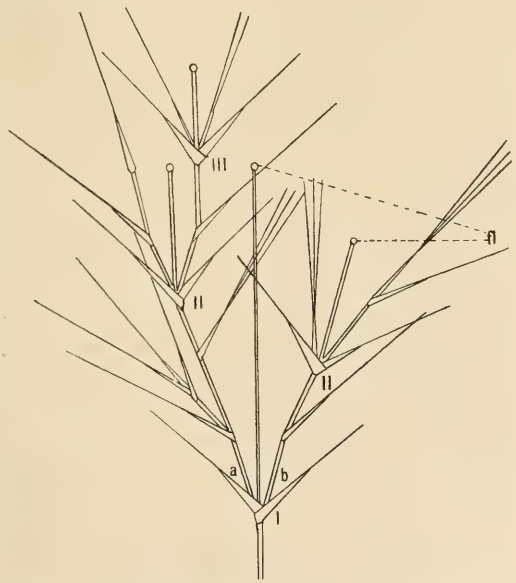

Figure 1.—Diagrammatic representation of inflorescent branch system; *a* and *b*, stronger and weaker shoots respectively; *I*, *II*, and *III*, successive generations of sympodial development; *fl*, flower.

When the upright or upward growing branches arrive at or near the surface of the water, their apices terminate in inflorescences, as shown diagrammatically in Text-fig. 1, consisting of a slender peduncle and a rhachis homologous to a spadix, the latter bearing always two flowers. From now on the inflorescent type of branching prevails. For from the axil of each of the two nearly opposite leaves subtending the peduncle (see p. 97 ff.) arises a secondary branch (Text-

fig. 1, *a* and *b*), which continues the growth of the stem. Of these branches, that in the axil of the upper leaf (Text-fig. 1, *a*) is invariably of stronger growth, exceeding considerably the branch on the other side of the floral axis. These axillary branches, after forming a few leaves, terminate in flowers again, and the process of branch formation is repeated. In this way, since the main axis is continued by the stronger branch, the system in the region of the flowers is sympodial. In most instances, however, the weaker axillary branch has a fairly vigorous development, as in Text-fig. 1, in which case the branching approximates a false dichotomy, and a characteristic fan-like form is thus often produced.

In Text-fig. 1 the branch *a* develops two ordinary leaves before it terminates in a flower. This brings the upper of the pair of subfloral leaves at the right side instead of the left, as at I. Such an arrangement as this is not as common as is the continual production of the stronger branches on the same side of the stem, but in this way also the fan-like form may be attained.

2. Comparative Study of the Branching of the Potamogetonaceae.

In Zannichellia, Campbell (1897, pp. 38 ff.) finds that the apex of the stem divides into two equal parts, one of which develops into the female inflorescence, while the other continues as the main axis of the stem. Farther on he says "the inflorescence is the result of the dichotomy of the main shoot, whose other member continues the growth of the axis." So that, although a sympodium is the ultimate result, it is attained by a dichotomy of the growing point, one of the branches becoming a male or female flower. Schumann's (1892) interpretation had been somewhat different from this, maintaining that the female inflorescence terminated the main axis and that the growth of the shoot was continued by an axillary branch arising in the upper of the two subtending leaves. The position of these leaves much resembles that of the subfloral leaves of Ruppia, so that if Schumann's idea were correct, the inflorescent branch system of Zannichellia would be a sympodium similar in origin and development to that of Ruppia.

Campbell's figures, however, show a vigorous, simultaneous development of the primordia of both flower and main axis, which lend to his theory a great deal of weight. In Ruppia the primordium of the axillary shoot arises much later than that of the flower, so that such a dichotomy as Campbell claims is here impossible. (See Pl. IX, figs. 54–56.)

Irmisch (1858) investigated the vegetative branching of Zannichellia and found it to be a pure sympodium as regards its horizontal axis. This develops beyond its second leaf into an upright shoot, which ultimately bears the flowers; at its base, however, from the axil of the second leaf, arises a branch which prolongs the horizontal axis. This again, after two leaves are given off, develops into an upright shoot and the horizontal axis is again repeated from a branch in the axil of the second leaf. This process goes on indefinitely, so that the horizontal axis is therefore merely a succession of generations of axillary branches and hence a pure sympodium.

The branching of Naias is peculiar, according to Campbell's (1897) interpretation. The leaves are developed approximately in pairs—one slightly below the other and larger. From the axil of this lower one a primordium arises which by dichotomy produces a flower and a lateral branch. The branch bears at its base a single leaf. The upper leaf of the original pair is sterile, so that the stem of Naias has its leaves apparently in whorls of three, with a branch and flower arising from each whorl. Apparently the apex of the main stem never terminates its growth, but goes on producing its pairs of leaves—one sterile and one fertile—so that the system is very unlike that of Ruppia.

Cymodocea, an entirely submerged marine genus, distinguished by its long ribbon-like leaves, very simple flowers and filamentous pollen, is placed by Ascherson (1889) next in order to Ruppia. In *Cymodocea nodosa*, Bornet (1864, pp. 15 ff.) describes types of branching which conform to those of Ruppia. The vegetative branching is monopodial, and a longitudinal section of the bud (l. c. Pl. IV, fig. 1) resembles very closely that of Ruppia. The flowers are terminal and the growth in length is continued by a lateral bud. It appears, however, that this bud is not necessarily one of the two buds nearest the flower.

In Zostera the rootstock is also monopodial, the inflorescent system being sympodial (Sauvageau, 1891, I).

Phyllospadix closely resembles Zostera (Dudley, 1893).

In Althenia (Prillieux, 1864), on the other hand, a genus resembling Zannichellia and found in Europe, Africa and Australia, the vegetative branching is sympodial, much as in Zannichellia. The growth of the rootstock is continued by successive branches from the horizontal axis which in each case itself becomes vertical and bears the flowers. The flowers are unisexual—the male terminating the upright axis or stem. In the axils of the two leaves subtending the male flower arise secondary branches, which bear male or

female flowers, but more often the latter. From these, branches of the third order arise, and in this manner a complex sympodial development is the rule.

Irmisch (1858) found that the vegetative branching of *Potamogeton lucens*, *natans*, *crispus*, *obtusifolius*, and *pectinatus* was purely sympodial as to the rootstock, just as it is in Zannichellia and Althenia. It is very probable that the other Potamogetons have the same system. As to the floral system the branching is sympodial.

Summary. The branching of Ruppia is of two main types:—a sympodial system occurring in the region of the flowers, and a monopodial system present in all other parts of the plant.

Zannichellia, Althenia, and Potamogeton have, however, a sympodial system in the case of the rootstock, but a purely monopodial development like that of Ruppia occurs in Cymodocea, Phyllospadix, and Zostera. With the exception of Zannichellia, where Campbell finds a true dichotomy, all these genera have a similar inflorescent branch system—a single or double sympodium formed from branches in the axils of the two characteristic subfloral leaves, or at any rate from a lateral bud as in Cymodocea.

C. Anatomical Structure

1. Growing Point.

In a good median section the growing point of the stem reveals the three divisions of primary tissue more or less clearly marked: the whole is covered by a layer of dermatogen; beneath this lies the periblem, composed of usually one layer and surrounding the three or four layers of plerome cells.

Text-fig. 2, besides demonstrating these meristematic divisions, shows an interesting very early stage in the development of the youngest leaf. Here the periblem on the right has undergone several divisions preparatory to the formation of the youngest leaf primordium, which is destined to appear at this region, opposite the next youngest leaf, L^{II}.

On the whole, the arrangement of cells and young lateral organs is very similar to that figured by Douliot (1890) for *Cymodocea aequorea*.

2. Stem Structures in the Vegetative Region.

a. Upright Stem.

In its internal structure the stem is remarkable in many respects, but chiefly because of the reduction and consolidation of the vascular system into what may be termed a single axial vascular bundle, if we except the two minute bundles situated in the cortex. The morphogenesis of this reduced structure, as well as the structure of the whole stem as regards its adaptability to its environment, will be considered more in detail later.

The epidermis surrounds a large zone of cortical parenchyma cells with a ring of lacunae in their midst; these cortical cells adjoin an endodermis, which encloses the axial vascular area (Pl. I, figs. 4–5; Pl. III, figs. 7, 8 and 9). The four parts —epidermis, cortex, endodermis and vascular system will now be described in order.

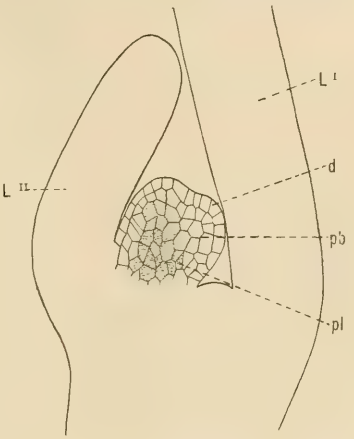

Figure 2.—Longitudinal section through growing point of stem, showing origin of youngest leaf primordium in the periblem; *d*, dermatogen; *pb*, periblem; *pl*, plerome; *L I*, *L II*, older leaves. × 210.

(1) Epidermis.

The epidermal cells are small in comparison with the cortical parenchyma cells and much smaller than the epidermal cells of the root (Pl. I, fig. 5). Their walls are thin, and yet thicker than the walls of the interior cells, the free wall being slightly thicker than the others. Occasionally these cells contain a small amount of chlorophyll.

As might be expected from a comparison with other submerged plants already investigated (Schenck, 1886), no stomata occur throughout the plant.

In the epidermis, rather regularly distributed over the stem, but especially abundant in the region of the nodes, are secretion cells, which are, however, more numerous in the leaf, and will be described more in detail there (see p. 90). These cells occur scattered here and there also in the cortex, and some may be seen in the axial vascular bundle.

(2) Cortex.

The typical cortical parenchyma cells are large in comparison with the cells of the epidermis, endodermis and vascular tissue; they are

rounded so that intercellular spaces often occur, and elongated in the direction of the length of the stem (Pl. I, fig. 5; Pl. III, fig. 7; Text-fig. 3). The majority of the cortical parenchyma cells show in an oblique view parallel horizontal stripes or bands on their side walls. A longitudinal section proves that this appearance is due not to bands of thickening, but to slight undulations (Text-fig. 3). These are not necessarily regular in size or distance apart; they may or may not occur all through the cell, and certain cells are apparently entirely without them. Their function is not clear. Similar undulations were observed by Caspary (1858) in several aquatic plants, notably in *Zannichellia palustris*. Prillieux (1864) has also noted them in the stem of *Althenia filiformis* and in the roots of epiphytic orchids.

Figure 3.—Longitudinal section of a portion of cortical parenchyma cells, showing undulations in the side walls. × 210.

Another point of general interest in the stem cortex is the occurrence of starch grains. These, as shown in Pl. I, fig. 5, are quite numerous. Their size evidently increases in the vicinity of the axial and cortical bundles and everywhere at the nodes. Irmisch (1858, p. 35) has found starch abundant in the Potamogetons and has described its occurrence and appearance in considerable detail.

In the cortex appear also the secretion cells noted in the epidermis, that is, they are apparently of the same nature, behaving in general in a similar way. They do not contain starch, as do most of the cortical cells, but are filled with fine granular contents and are especially abundant at the nodes. Bornet (1864, pp. 40–41) has noted cells evidently quite similar in the cortex and vascular tissue of Cymodocea, filled with a "liquide oléagineux, un peu teinte de jaune, tout-à-fait semblable à celui que renferment les cellules épidermiques des anthères."

In describing the cortex we may for convenience divide it into three portions: (a) an outer zone of cells, compactly arranged and bounded on the outside by the epidermis; (b) a central area, with a large portion of its territory occupied by a ring of lacunae or air spaces; and (c) an interior zone of cells limited on the inner side by the endodermis (Pl. I, fig. 5).

(a) *Outer cortex.*

The outer portion of the cortex consists of two or three layers of cells (Pl. I, fig. 5 *oc*; Pl. III, fig. 7). The cells of the outermost

layer are much larger than those of the epidermis, but partake somewhat of the nature of the latter in their slightly thickened walls. Toward the outer part of this cortical region intercellular spaces rarely occur: instead the triangular prismatic areas which the spaces would occupy are filled with thickening and probably supplement the firmness imparted to the stem by the epidermis.

It is in this outer portion of the cortex that two small vascular bundles occur, which may be termed cortical bundles (Pl. I, figs. 4, 5, *cb*). An account of these will be given in connection with the vascular system.

Toward the interior of this zone the cells increase in size, and intercellular spaces begin to appear.

(b) *Middle cortex.*

The most striking feature of the middle area of the cortex is the ring of large air spaces or lacunae (Pl. I, figs. 4, 5, *mc* and *la*; Pl. III, fig. 7). These originate schizogenously by a splitting apart of the walls of adjacent cells when these are in a very young stage, and subsequently they become much enlarged. A ring of from twelve to eighteen is disposed in a fairly symmetrical way in this central part of the cortex. As a rule somewhat elongated radially, they are separated from each other laterally by a single column of cells. In length up and down the stem they extend from node to node, no diaphragms being stretched across as in the leaf lacunae. Communication through the node is maintained by means of small intercellular spaces.

Between the lacunae and the small intercellular spaces occurring near the inner and outer limits of the cortex lie many air spaces of intermediate size, so that although the large lacunae appear quite distinct on account of their large size and fairly regular arrangement, yet gradations exist between them and the small triangular intercellular spaces (Pl. I, fig. 5).

(c) *Inner cortex.*

The interior zone of the cortex, terminating with the endodermis (Pl. I, fig. 5, *end*), is a good deal similar to the outer zone. The cells and intercellular spaces gradually decrease in size, and the latter also in frequency, toward the endodermis, while the cell walls gradually increase in thickness.

A striking peculiarity of the cells of this inner cortical zone is their chlorophyll content, which is very noticeable in freehand sections from fresh stems. It was definitely ascertained that the chlorophyll grains belong to these cells and were not drawn inward from the epidermis by the razor.

(3) Endodermis.

The endodermis is a fairly regular layer of cells surrounding the central vascular region (Pl. I, fig. 3). On the application of concentrated sulphuric acid all the walls of the endodermal cells become beautifully undulated, the radial walls showing a stronger suberization. In many cases the ring of cells outside of the endodermis is also quite strongly suberized and therefore withstands to a considerable extent the action of the sulphuric acid (Text-fig. 4). No U-shaped stripes of thickening appear on the walls, such as were seen by Schenck (1886) in *Potamogeton pectinatus* and other species. Although a banded appearance is produced in a slightly oblique view, a longitudinal section shows that it is due merely to the slightly undulating walls, essentially as has been shown in the cortical cells. The radial walls, however, are slightly thickened uniformly.

Figure 4.—Cross section of portion of endodermis and next outer ring of cells treated with concentrated sulphuric acid, showing slightly thickened radial walls. × 400.

(4) Vascular System.

One of the most interesting features of the stem is its remarkably simple vascular system. This comprises two small cortical bundles and a larger central bundle (Pl. I, fig. 4; Pl. III, fig. 7). I shall describe first the course of these bundles, and then turn to a description of their anatomical structure.

(a) *Course of Vascular Bundles.*

The course taken by the vascular bundles in the stem is very simple. The main central bundle travels in the center of the stem, and at each node sends off two branches in the manner figured (Pl. V, fig. 17)—a large branch to the lateral member which almost invariably occurs at each node, and a smaller contribution to its subtending leaf. This is repeated at each succeeding node until the floral region is reached. Here the main bundle continues to its termination in the rhachis, but gives off on each side a couple of branches to the lower and upper subfloral leaves with their axillary members in turn. This is simply a repetition of the process occurring at then odes, except that here, between the lower and upper subfloral leaves, the node is practically obliterated (Pl. V, fig. 18). This arrangement, at least in the vegetative region, is much like that of *Potamogeton pectinatus*, described and figured by De Bary (1884, p. 273).

The course taken by the cortical bundles, although simple, is not quite as evident. The cortical bundles are entirely independent of the central bundle, never connecting with it, so far as I have been able to ascertain. Their position can be best shown by the use of figures selected from a series of cross sections. A cross section in the region of a node, just below the point where the leaf is given off, is represented in Pl. V, fig. 19. Here the cortical bundles are situated in the outer cortex, not quite diametrically opposite each other. This figure also shows the axial bundle somewhat dilated radially. Pl. V, fig. 20 shows the edges of the leaf sheaths appearing at the cleft at the upper side of the figure. The cortical bundles occupy about the same position as before, but the axial bundle is commencing to give off its two branches—to the leaf and axillary branch. In Pl. V, fig. 21 the leaf sheaths are still more separated from the stem; the two large leaf and branch bundles are now distinct from the axial stem bundle; the cortical bundles have moved outward slightly, and a new cortical bundle appears nearer the central bundle. Since the section is cut slightly obliquely, and the right side represents a portion higher up in the stem, only one of the pair of new cortical bundles thus appears. Pl. V, fig. 22 shows both, however, and also represents the former pair of cortical bundles as moving gradually into the still further separated leaf. Pl. V, fig. 23 shows the leaf with its lateral (cortical) bundles, separate from the stem, and fig. 24 does the same for the branch which it subtends.

It is clear, therefore, that the cortical bundles of the stem furnish the lateral nerves of the leaf. It will be seen also that not only do the cortical bundles have no connection with the axial bundle, but also that a new pair arises at each node to pass into the leaf at the node next higher up. After a careful examination, I find absolutely no connection between these successive pairs of cortical bundles.

Although the figures and description of De Bary (1884, p. 274) for *Potamogeton crispus* seemed to present an arrangement similar to the above, the work of Chrysler (1907), which appeared while this paper was being prepared for publication, corrects De Bary's account but confirms my investigation of *Ruppia maritima.* Chrysler's conclusion (l. c. p. 171) is undoubtedly correct that "this condition has in all probability been derived by reduction from that in which the cortical bundles joined the central cylinder at the next node below the insertion of the leaf to which they belong."

The cortical bundles of *Zostera marina* (De Bary, 1884, p. 275;

Sauvageau, 1891 I; Chrysler, 1907) are similar to those of Ruppia, but are continuous up and down the cortex and send a branch to the central cylinder at the nodes.

(b) *Structure of Vascular Bundles.*

Anatomically the cortical bundles in a young stage consist of small, closely packed cells, which are all tracheids or tracheae (Pl. III, fig. 8). No sieve tubes can be distinguished (Text-fig. 5). At a later stage (Pl. I, fig. 5; Text-fig. 6) these small elements have for the

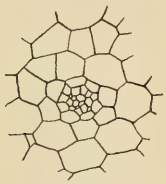

Figure 5.—Cross section of cortical bundle, before dissolution of its vascular elements. × 210.

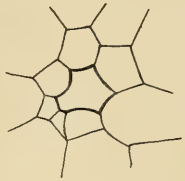

Figure 6.—Cross section of cortical bundle, after dissolution of its vascular elements. × 300.

most part been resorbed, so that only a passageway remains, except at the nodes, where they remain intact.

In structure, the central cylinder is composed of a central xylem region surrounded by a zone of phloem. The xylem is in a young stage represented by a group of tracheae at the center, which, however, very early in the development of the stem, become pulled apart and disorganized except at the nodes, where they are conspicuous in the mature stage. The resulting space, then, is a lysigenous cavity, and does not represent an enlarged cell (Pl. I, fig. 3). The thickenings of the tracheae are mostly annular, although spiral and other forms may occur (Text-fig. 7). Occasionally these thickenings may be found lying loose

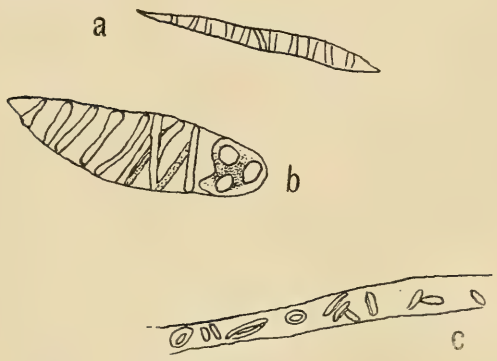

Figure 7.—Tracheae and tracheids from axial vascular bundle of stem: a. tracheid with annular thickenings; b. tracheid with annular, spiral, and pitted thickenings; c. disorganized trachea with thickenings lying in the cavity. × 1350.

in the central lysigenous opening. In sections of the stem it appeared as if tracheids were also present, especially at and near the nodes, possessing the same characters as to their thickenings as the tracheae, but showing cross walls (Text-fig. 7 *a*, *b*).

Surrounding the central cavity are thin-walled xylem parenchyma (Pl. I, fig. 3). Just outside of these lies the phloem region, the boundary between the two being impossible to determine on account of the apparently identical characters of the xylem and phloem parenchyma.

In the phloem zone are distributed the sieve tubes, with their companion cells, in an irregular ring in much the same way as in Zannichellia (Schenck, 1886). As a rule, the sieve tubes are larger than the surrounding cells, and on this account and because of their arrangement in a ring, each with its companion cell, they stand out quite clearly even in freehand sections. Between them and the endodermis lie one or occasionally two layers of parenchyma cells (Pl. I, fig. 3).

One noteworthy feature of the phloem region is that in the vicinity of the node, i. e. immediately before and after the branches are given off from the central cylinder, it is localized into four distinct symmetrically situated portions (Text-fig. 8), although this is never evident in the internodal region. Such an arrangement would be expected when one considers the true nature of this fibrovascular area, as described below, and compares it with certain Potamogetons which reveal this character more distinctly (Schenck, 1886. pp. 40–41 and figures 35, 36 and 38), and with *Zostera marina* (Chrysler, 1907, p. 172 and fig. 29).

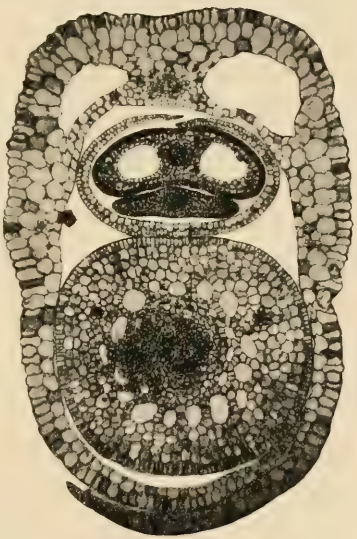

Figure 8.—Photomicrograph of cross section of stem, &c., similar to Pl. III, fig. 8, but cut at a higher plane and near a node; showing localization of phloem into four regions in central cylinder of stem. × 35.

In his work already cited, Schenck (1886, pp. 27 ff.) reviews in a most admirable manner the various interpretations of the concentric type of bundle as it exists in water plants. He concludes with Sanio and Russow that it represents phylogenetically not a single

bundle, but the product of the gradual centripetal union of many stem bundles, and is therefore not comparable to the concentric bundle of the majority of the Gleicheniaceae, for example. This is true both of mono- and dicotyledonous water plants.

In support of this theory Schenck shows how there exists at the present time in different aquatic and amphibious species, every gradation from the typical bundle arrangement common to land plants to the simplest structure as exemplified in the submerged aquatics. He says, "Im Laufe der phylogenetischen Entwicklung rückten infolge immer weiter gehender Anpassung der Structur an die Lebensweise der Pflanze unter Wasser diese Leitbündel bei gleichzeitiger Reduction des Xylems nach der Axe zusammen zu einem gemeinsamen Strang, in welchem die Xylemteile nach und nach zu einem einzigen axilen Körper verschmolzen, während die Phloemteile, ihre normale Lage nach außen beibehaltend, zu einer Ringzone sich vereinigten."

According to this interpretation therefore, Ruppia is descended from a form with four distinct main vascular bundles, traces of which are still apparent in the four phloem regions at the nodes; for here, as is generally admitted, ancestral characters are wont to appear.

Summary. The stem is composed of a thin walled epidermis; a loosely constructed cortex, containing as its principal feature a ring of radially arranged lacunae, and also two small bundles ending in the cortex—fibrovascular connections with the leaf sheaths; and a well defined endodermis, surrounding a very simple axial vascular region of a concentric structure, the appearance of which at the nodes indicates its reduction from four vascular bundles.

b. Rootstock.

The branching of the rootstock, or horizontal axis, as already stated, conforms strictly to the monopodial type, although torsion and the decay of the leaves often renders this obscure.

In its internal structure, as would be expected, it agrees with the stem (Pl. III, fig. 9). No points of difference were noted, except that sometimes the cells are somewhat larger than is customary in the upright axis, and often contain a large amount of starch.

The main differences between this and its morphological equivalent, the upright axis, are its horizontal position and the occurrence of roots at the nodes

3. Stem Structures in the Floral Region.

Three forms coming under the category of stem are found in connection with the production of flowers and fruit: (a) the peduncle, or the stalk of the inflorescence, (using this term in its narrower sense); (b) the rhachis or axis of the inflorescence, which is joined to the apex of the peduncle and bears the sessile flowers; (c) the stipe, a stalk which acquires its full development subsequent to the fertilization of the ovule and bears the mature fruit at some distance from the rhachis.

These three parts will be considered in order.

a. Peduncle.

(1) General Characters.

At the time of blooming the peduncle is short, about 2.5 cm., in length, and is raised nearly its whole length vertically above the surface of the water. About the time that the pollen is shed and the anthers fall off, the peduncle becomes horizontal, floating on the surface of the water. From now on it commences to elongate, presumably by simple stretching of its cells, as no meristematic regions were found to prove the contrary. It elongates until in some cases it attains great length. One specimen I measured was 18.2 cm. long. Elongation takes place whether fruit is matured or not, and the length is apparently just as great in either case. Indeed, the specimen just mentioned bore no fruit. The average length of the peduncle when no fruit was matured was 5.39 cm. The average length in 80 specimens when ovules were matured was 4.9 cm. On the whole, therefore, the average length of the extended peduncle is about 5 cm. or about twice that at the time of flowering.

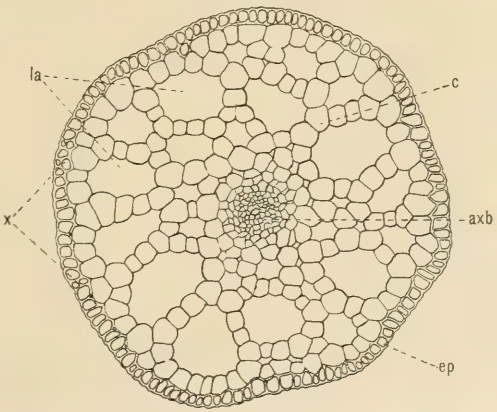

Figure 9.—Cross section of peduncle, showing at *x* the apparently double epidermal cells; *ep*, epidermis; *la*, lacunae; *c*, cortex; *axb*, axial bundle. × 185.

(2) Anatomical structure.

In general, the anatomical structure of the peduncle is very similar to that of the leafy stem (Text-fig. 9; Pl. VI, fig. 34). The following points, however, are noteworthy:—

1. As would be expected, no cortical leaf trace bundles are present.

2. The central vascular area is very similar to that of the stem. The tracheae in the center are pretty well disorganized, which is natural when one calls to mind the considerable extension of the peduncle.

3. The lacunae are more numerous and much larger in proportion to the diameter of the peduncle than in the stem (Text-fig. 9; Pl. VI, fig. 34).

4. In comparison with the stem the epidermis has slightly thicker walls, and small intercellular spaces may occur between it and the subjacent layer, an appearance which one never sees in cross sections of the stem (Text-fig. 10).

5. Occasionally some of the epidermal cells have a peculiar halved appearance, as if a periclinal wall divided an ordinary epidermal cell into two parts. This is due probably not to a division in the epidermal cell, but to the fact that a small subepidermal cell is wedged up close to a small epidermal cell (Text-fig. 10).

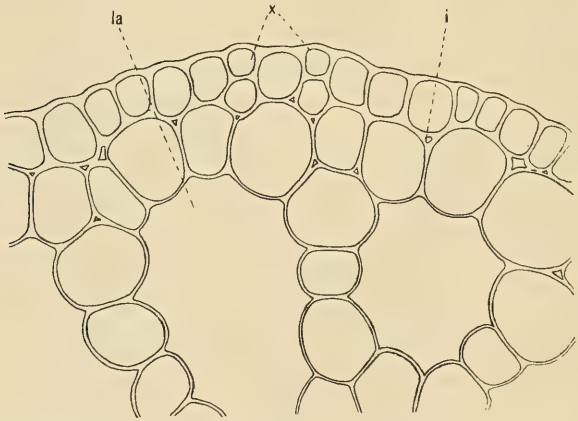

Figure 10.—Portion of cross section of peduncle; *x*, apparently double epidermal cells; *la*, lacunae; *i*, intercellular spaces. × 300.

On the whole, the main differences between this structure and that of the ordinary stem are its lack of cortical bundles and its lighter construction. The latter is explained when one recalls the fact that the peduncle for a great period of its existence floats, and hence its specific gravity must be small.

(3) Coiling of the peduncle.

Sooner or later the peduncle becomes spirally coiled, drawing the fruit, if any is matured, below the surface of the water. Some individuals exhibit this characteristic more markedly than others. Often, in fact, the peduncle is fairly straight. In case the coiling takes place, it is due to the cells on that side of the peduncle which will form the outer side of the spiral becoming longer than those on the inner side. This difference in length was ascertained in several specimens by actual measurement of the cells. Such curvatures as this occurring in plants are most often, as Strasburger (1908, p. 269) has explained, due in like manner to unequal growth.

b) Rhachis.

Here the internal structure is practically the same as in the peduncle. No appreciable elongation takes place as in the peduncle, and, therefore, the tracheae are not disorganized to such an extent. At the point of attachment of the stamens the rhachis is practically triangular in outline (Pl. III, fig. 11). The single axial vascular bundle sends a branch to each stamen and to each of the four pistils of a flower (Pl. III, fig. 12). This axial vascular region terminates with the branch sent to the uppermost stamen (Pl. III, fig. 12), the most distal member of the inflorescence, and does not therefore have a blind ending at the end of the rhachis.

The termination of the rhachis is simply a rounded knob (Pl. III, fig. 12).

All through the rhachis, in the interior as well as in the epidermal tissue, the "secretion" cells are abundant.

c) Stipe.

Although the pistils are termed sessile, and correctly so from a macroscopic standpoint, early in their development, before fertilization (Pl. III, fig. 12), considerable tissue is formed between the ovule and the rhachis by a region which remains meristematic for some time. At length the cell division ceases, and the cells stretch out, forming a stalk of considerable length, having at its end the mature fruit (Pl. IV, fig. 13). This stipal development is correlative; when no fruit is developed, the stipe is also wanting.

Pl. IV, fig. 14, which shows the secretion cells in the epidermis of the stipe, represents a stage when the cells are still quite young and short.

In its internal structure the stipe reveals no marked differences from the stem (Pl. IV, fig. 15). As in the peduncle, the cortical bundles are lacking. The lacunae are less pronounced than in the peduncle. The apparently halved epidermal cells occasionally appear,

and in places the subepidermal layer is thick-walled and constructed much like the epidermis (Pl. IV, fig. 16). As a whole, the structure shows greater strength than the peduncle.

4. Brief Comparative Study of the Stem Anatomy of the Potamogetonaceae.

Zannichellia (Campbell, 1897) and Althenia (Prillieux, 1864) perhaps most closely resemble Ruppia in their cauline structure, although they possess no cortical bundless. *Potamogeton pectinatus* (Schenck, 1886) also, which externally resembles Ruppia so closely, internally reveals a very similar stem anatomy. Moreover, the Potamogetons possess cortical bundles lacking in Zannichellia and Althenia. Cymodocea (Bornet, 1864), appears to differ mainly in having a thicker stem and a ring of small cortical bundles with lacunae between these and the axial vascular area.

In its vascular system Zostera (Sauvageau, 1891. I.) shows close relationship to Ruppia. *Z. capricorni* and *Z. nana* have one cortical bundle on opposite sides of the stem, as in Ruppia (Sauvageau, 1891). *Zostera marina* (Chrysler, 1907. p. 172, fig. 29) is also similar. In other species these bundles are more numerous. The bundles run free the whole length of the internode, unite with the central area at the node and send out branches which become the lateral nerves of the leaves. The central vascular area appears composed of four fibrovascular strands, the phloem parts isolated and separated, and the xylem bundles united into an axial strand.

Leaf

A. Enumeration of Kinds of Leaves

Of Strasburger's (1908, p. 26) four categories of leaves, three occur in Ruppia:—the scale leaves, small specialized structures at the base of every branch (Pl. II, fig. 6, *vsl*; Text-figs. 19–20, *vsl, fsl*); secondly, the ordinary long, narrow foliage leaves; and finally, the subfloral leaves, belonging properly to the category of bracts, a pair of which is borne at the base of the peduncle (Text-figs. 19–20, *up. sfl, low. sfl*). Since the flower is naked, there are no floral leaves.

B. Arrangement

An investigation of the position of the leaves throughout the plant reveals the following:

1. The general leaf arrangement is distichous (Pl. I, fig. 2; Pl. II, fig. 6), as in other members of the Potamogetonaceae so far as known, with the exception of *Potamogeton natans* and *Potamogeton lucens*, where a several ranked arrangement sometimes occurs (Irmisch, 1858 and Ascherson, 1889).

2. A single plane, therefore, will intersect all points of leaf insertion on any stem (Pl. I, fig. 1; Pl. VI, fig. 25).

3. Moreover, on all branches, this plane of leaf insertion coincides with that of the main stem, a feature which combines with the methods of branching to produce the characteristic flat, fan- or sickle-shaped plants, a condition already noted in the Potamogetonaceae by Ascherson (1889) (Pl. I, fig. 2; Pl. II, fig. 6).

4. The first, or basal leaf of every branch, which is in all cases a scale leaf, originates on that portion of the branch opposite to the subtending leaf—i. e., with its back toward the main axis of the shoot (Pl. II, fig. 6, *vsl*). No internode is placed between it and the subtending leaf, so that it is therefore exactly opposite the latter.[1]

5. The second leaf of every branch, in all cases a foliage leaf, is developed on the side of the branch adjacent to the subtending leaf, and thereafter ordinary foliage leaves of the branch proceed in regular distichous order (Pl. II, fig. 6, $l_1^{(I)}$, $l_2^{(I)}$, &c.).

In an account of the leaf of Ruppia I shall describe the three sorts of leaves, beginning with the ordinary foliage leaves, taking up next the subfloral leaves, and concluding with the scale leaves.

C. Ordinary Foliage Leaves

General Characters. The ordinary foliage leaves are "ribbon-shaped"; long (7—17 cm.), and very narrow, (about 1 mm.) (Pl. I, fig. 2; Pl. II, fig. 6). Although to the naked eye the margins appear entire, the microscope reveals at the apex a large number of one- to three-celled teeth, and these, with increasing distances between them, extend a considerable distance down the margins of the leaf (Pl. VI, fig. 26; Text-fig. 11). Upward from the base of the leaf, on each side, extending for 13–27 mm. are thin translucent appendages,

[1] Goebel (1898, pp. 68—69) says, however, in speaking of the phyllotaxy of axillary branches in general, that, due to mechanical causes in the bud, "die bei weitem häufigste Stellung der beiden ersten Blätter des Axillartriebs eine *laterale* ist, und erst die folgenden Blätter *median* oder mehr oder weniger schief gestellt sind."

which I have termed the stipular sheaths (Pl. I, fig. 2; Pl. II, fig. 6). In external appearance the leaves very closely resemble those of *Potamogeton filiformis* and *Potamogeton pectinatus*, both also typical submerged plants (Morong, 1893). The leaves of Zannichellia and Althenia are also macroscopically very similar: those of all species of Naias are much shorter with strongly serrate or toothed margins.[1]

Development of the Foliage Leaf. Different stages of leaf development are represented in Pl. I, fig. 1; Pl. VI, fig. 25, longitudinal sections of a vegetative bud, where the youngest leaf is the protuberance at one side of the growing point (L^{VIII} in Pl. I, fig. 1). The next older leaf primordium, shown on the right of the growing point (Pl. I, fig. 1, L^{VII}), has already slightly elongated, until now it extends beyond the growing point. Successively older stages are represented by L^{VI}, L^{V}, L^{IV}, &c.

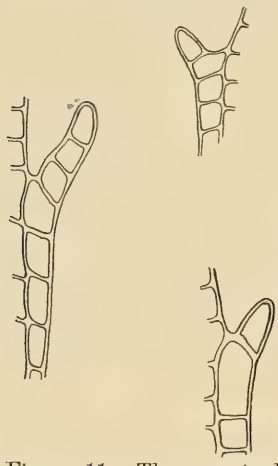

Figure 11.—The marginal leaf teeth, showing variation in cell arrangement. × 300.

Pl. VII, fig. 43 represents a transverse section through a similar bud cut through about the region of the line *a b* in Pl. I, fig. 1. Therefore, we find here the different members in exactly the same orientation as in Pl. I, fig. 1. Thus, the outermost leaf, L^{I}, embraces with its sheaths all the internal complex, just as is shown by L^{I} with its sheaths in Pl. I, fig. 1. The next inner member is $l_1^{(I)}$, or the lowest and largest foliage leaf of the axillary bud of L^{I}; then a section through the apical portion of the scale leaf which envelops this axillary bud; next the leaf sheaths of the next upper main leaf, L^{II}, appear, which brings us to a cross section of the central stem: without going into more detail it is sufficient to note that the remaining parts may be correlated to their corresponding longitudinal sections in the same way. The line *a b*

[1] All these species belong to Hansgirg's (1903) "Vallisneria-Typus der Strömungsblätter," a physiological group showing little differentiation into blade and petiole and characterized by the lack of cuticle, hair structures and stomata, by the absence of any considerable amount of supporting tissue, and by the ribbon-like, isolateral form.

in Pl. VII, fig. 43 represents the approximate plane in which a section similar to that in Pl. I, fig. 1 and Pl. VI, fig. 25 would be cut.

With the help of these sections and other similar serial preparations, I have found that the course of development and distribution of growth in the ordinary foliage leaf is approximately as follows: the leaf primordium first appears as a mere swelling at one side of the growing point, Pl. I, fig. 1, L^{VIII}; this protuberance soon differentiates into two parts, an "upper leaf," elongated in the direction of the growth of the shoot, and a "leaf base,"—to use the terms of Eichler, 1865—consisting of lateral protuberances on each side of the base of the "upper leaf" and extending part way around the shoot axis (Pl. VII, fig. 39). This arrangement is also shown, though not very clearly, by Pl. VI, fig. 28. The "upper leaf" will produce the leaf blade and the "leaf base" the leaf sheaths. The upper leaf now elongates rapidly, being composed entirely of embryonic tissue, and the succeeding stages are essentially those described by Prantl (1883): the cells at the apex are the first to commence extension to their mature size, and this stretching gradually proceeds toward the base of the leaf. The final developmental stage is marked by a considerable growth of the sheaths due to the intercalary growth of the leaf, which Goebel (1898, p. 518) states is so characteristic of monocotyledonous leaves.

A point of interest here is the comparative large size of the sheath rudiments at the first segmentation of the leaf primordium (Pl. VII, fig. 39), a circumstance which will be discussed below under the heading of the leaf sheath.

For purposes of further description, it is best to divide the leaf into two parts,—the blade and the sheaths, assuming the blade to be that part of the leaf from the sheaths to the apex (Pl. I, fig. 2; Pl. II, fig. 6).

1. The Leaf Blade.

A cross section of a leaf, made above the region of the sheaths, is represented in Pl. VII, fig. 43, $l_1^{(I)}$. An epidermis of comparatively narrow cells, a subepidermis of wider cells, a single axial vascular bundle with one subsidiary bundle running along each leaf margin, a lacuna or air space on each side of the axial bundle, and a few extra interior layers of parenchyma cells toward both edges of the leaf and surrounding the vascular bundle comprise, in brief, the internal structure of the leaf blade.

a. Epidermis.

(1) Chloroplasts.

An interesting point brought out by a study of the epidermis, and shown especially well in the living condition, is the fact that here most of the photosynthesis is carried on, for the cells contain large numbers of chloroplasts (Text-fig. 12). The discussion of the causes of this condition, being of an ecological nature, will be postponed for the present.

(2) Marginal Teeth.

The teeth, mentioned above, p. 88 (Pl. VI, fig. 26; Text-fig. 11), have already been observed in the leaves of *Ruppia maritima* by Sauvageau (1891, II, p. 209), who says, "à son sommet [i. e. of the blade] la plupart des cellules terminales se prolongent en dents arrondies composées de 1–2–3 cellules. Des dents semblables, mais plus espacées, se retrouvent sur les bords latéraux du limbe et font légèrement saillie." In a young stage, as in Pl. VII, fig. 39, the teeth appear mostly at the end of the leaf primordium; later they may be found down the margins of the leaf anywhere from $\frac{1}{2}$ to $\frac{3}{4}$ of the whole distance from the apex. Finally, in the adult leaf they rarely extend more than $\frac{1}{4}$ of the distance from the apex.

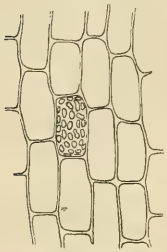

Figure 12.—Portion of epidermis of leaf, showing chloroplasts. Drawn from living leaf. × 335.

(3) Secretion Cells.

In the epidermis I have observed also the cells referred to by Sauvageau (1891, II, p. 209) as "cellules sécrétrices," containing, in alcoholic material, a granular or a homogeneous content of a brownish color, and somewhat larger than the ordinary epidermal cells (Pl. VI, fig. 30; Pl. III, fig. 8). They appear to be identical in nature with those of the stem. Although Sauvageau asserts that they are most abundant at the edges and at the apex of the leaf, yet they appear to me often to increase in numbers towards its base, including that part which adjoins the sheaths, as well as in the sheaths themselves (Pl. VI, fig. 25). According to Sauvageau these peculiar cells occur also in Posidonia, Cymodocea and Halodule. He has ascertained the presence in them of tannin, probably in combination. In my permanent slides their contents were almost invariably granular, assuming, with the triple stain, either a crimson or a brilliantly refracting yellow color—more often the latter. With ferric chloride the contents stained a brownish black and the same result was given on treatment with potassium bichromate.

These reactions confirm Sauvageau's assertion that these cells are tanniferous. As is well known, tannin is a common byproduct in plants, and in this case is possibly deposited in special cells on account of the difficulty of its diffusion through the epidermis. That these tanniferous cells should be more abundant toward the base of the leaf is natural, for it would be more economical for the plant to devote as many as possible of the cells in the upper part of the leaf to photosynthesis.

(4) Absence of Stomata.

Another peculiarity of the epidermis is the absence of stomata, which will be discussed later (p. 118).

b. Subepidermal Layer.

Below the epidermis, at all parts of the leaf, is a distinct layer one cell thick, which I have termed the subepidermal layer (Pl. VII, fig. 43), composed of cells about twice the width, tangentially, of those of the epidermis; and longitudinally, i. e. running the length of the leaf, many times longer than the epidermal cells (Text-fig. 13). This layer contains a few chloroplasts (cf. Sauvageau, 1891, II, p. 293).

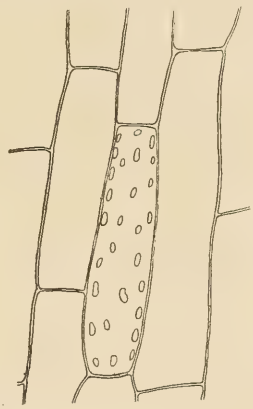

Figure 13.—Portion of subepidermal layer of leaf blade, showing a few chloroplasts. Drawn from longitudinal section cut from living leaf. × 335.

c. Vascular System.

The vascular system of the leaf is extremely simple. Three strands of conducting tissue are present—one large axial and two small marginal.

(1) Course of Vascular Bundles.

These three vascular strands enter the leaf separately at its insertion on the stem. The axial bundle maintains a median position and extends to very near the tip of the leaf (Pl. VI, figs. 26, 30; Pl. VII, fig. 43); the two lateral bundles enter one on each side of this axial bundle, and throughout their extent run parallel to it (Pl. VII, fig. 43, *lb*).

In the region of the sheaths each of these lateral bundles runs along the edges of the leaf proper, just at its line of junction with the sheaths, and above the leaf sheaths they retain this marginal position. I can confirm Sauvageau's (1891, II, p. 210) observation that they do not unite with the median bundle near the apex of the leaf, but disappear—according to my preparations, about 10 mm. from the apex.

(2) Structure of Vascular Bundles.

The axial bundle contains two or three annular tracheae in its young stage, which generally break down in the mature leaf to form an open passageway; surrounding this portion are phloem cells and parenchyma, difficult to distinguish on account of their low degree of differentiation, and about the whole axial bundle is a pretty definite endodermis, which Sauvageau has also noted. The structure of the two lateral bundles is extremely simple, consisting merely of a very few small conducting cells (Pl. VII, fig. 43, *l b*).

d. Lacunae.

On each side of the central bundle, separated from it by two or three layers of parenchyma, are the lacunae (Pl. VII, fig. 43, *l a*). In mature leaves these are of the shape of flattened cylinders, extending longitudinally through the leaf, and divided into compartments by transverse, sometimes oblique, perforated, one-layered plates of roundish cells (Pl. VI, fig. 25; Text-figs. 14–15). The perforations are round intercellular spaces, occurring regularly at the

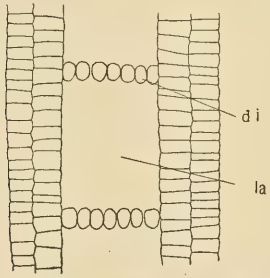

Figure 14.—Longitudinal section of lacuna, showing cross sections of diaphragms; *d i*, diaphragm; *l a*, lacuna. × 185.

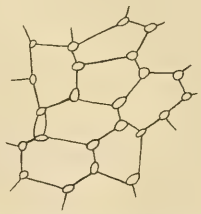

Fig. 15.—Surface view of one of the diaphragms which separate the leaf lacunae into compartments. The small circular outlines represent spaces between the cells. × 350.

angles of the cells and affording communication for the air or gases from one compartment to the next.

e. Comparison with Other Potamogetonaceae.

The anatomy of the leaf of *Potamogeton pectinatus*, a plant so much like Ruppia in external appearance, is almost a duplicate of the leaf structure of Ruppia (Schenck, 1886, p. 16 and figure 11 *d*). The other species of Potamogeton show differences more or less great, according to the shape of the leaf and the external conditions. The leaves of *Zannichellia palustris* (Schenck, l. c.) and *Althenia*

filiformis (Sauvageau, 1891, II, p. 259, and Prillieux, 1864) are very similar, the main difference being the absence in both of the marginal bundles, although Althenia has in place of these, small groups of fibrous cells. Althenia is, moreover, further distinguished by a rather large number of lacunae of various sizes.

The leaves of Zostera, Phyllospadix, Posidonia, Cymodocea and Halodule, show greater differences, of all of which, together with the remaining Potamogetonaceae, Sauvageau has made an excellent comparative study in his "Feuilles des monocotylédones aquatiques" (1891, II).

2. The Stipular Sheaths.

a. Structure.

At every node the leaf envelops the stem by means of basal sheaths composed of only two layers of cells. These cells lack chlorophyll and become very minute at the free edge of the sheath (Pl. I, fig. 2; Pl. VII, fig. 43, *s h s*).

b. Development.

I have already (p. 89) mentioned the fact that the development of the sheath rudiments in the young leaf primordium is quite marked. From the record of measurements (see Table p. 94) of the length of sheaths at different stages of leaf development there is manifested a certain periodicity in the growth of the sheath. Thus its percentage of the whole leaf length in a very early stage is high, as is shown in Nos. 1 and 2 and Pl. VII, fig. 39;[1] next, during the special growth of the leaf (see p. 89) this percentage noticeably decreases, in some cases to a very marked extent;[2] finally, due to the ultimate basal intercalary growth, the proportional size of the sheath again increases until in the mature leaf the proportional length of sheath to entire leaf averages about 1 to 6 (Table, Nos. 27–38).

Although, even by making considerable allowance for error, the data in the table are not at all uniform, as is natural, yet they do bring to light with no uncertainty the large comparative development of sheath both at the beginning and at the end of leaf growth.

c. Function.

That this periodicity in sheath development is related to the principal function of stipules, that of protection of younger parts,

[1] Such an early enlargement of sheath is mentioned by Van Tieghem (1898, pp. 250–251), who speaks of it as quite general.

[2] Possibly the very low percentages are results of environmental influence, e. g. position of leaf on shoot, surrounding leaf sheaths, &c.

TABLE
of
COMPARATIVE LENGTH OF SHEATH
IN THE VARIOUS STAGES OF LEAF DEVELOPMENT.

Description of specimen	No. of specimen	Length of entire leaf	Length of sheath	Approximate percent. of sheath to leaf length
Dissected from living plant	1	.14 mm.	.0525 mm.	37.5 %
„ „ „ „	2	.341 „	.0875 „	25 6 „
From prepared slide	3	.586 „	.0875 „	14.9 „
„ „ „	4	.735 „	.11 „	14.9 „
„ „ „	5	.8137 „	.1487 „	18.2 „
„ „ „	6	.8137 „	.1225 „	15. „
„ „ „	7	.8575 „	.1575 „	18.3 „
„ „ „	8	1.137 „	.096 „	8.4 „
Living specimen	9	1.382 „	.096 „	6.9 „
From prepared slide	10	1.41 „	.122 „	8.6 „
„ „ „	11	1.47 „	.19 „	12.9 „
„ „ „	12	1.54 „	.11 „	7.1 „
„ „ „	13	1.80 „	.17 „	9.4 „
Living specimen	14	2.275 „	.262 „	11.5 „
From prepared slide	15	2.362 „	.227 „	9.6 „
„ „ „	16	2.458 „	.166 „	6.7 „
„ „ „	17	3.745 „	.105 „	2.8 „
Living specimen	18	11.14 „	.315 „	2.8 „
„ „	19	11.81 „	.525 „	4.4 „
„ „	20	22. „	1. „	4.5 „
„ „	21	31. „	1. „	3.2 „
„ „	22	38.6 „	3.6 „	9.3 „
„ „	23	61.9 „	9. „	14.4 „
„ „	24	66.6 „	4.6 „	6.9 „
„ „	25	70.4 „	1.4 „	1.9 „
„ „	26	70.9 „	2.9 „	4. „
Living matured specimen	27	102. „	14. „	13.7 „
„ „ „	28	109. „	15. „	13.7 „
„ „ „	29	116. „	18. „	15.5 „
„ „ „	30	116. „	23. „	19.8 „
„ „ „	31	118. „	20. „	16.9 „
„ „ „	32	125. „	25. „	20. „
„ „ „	33	130. „	25. „	19.2 „
„ „ „	34	130. „	25. „	19.2 „
„ „ „	35	133. „	25. „	18.7 „
„ „ „	36	134. „	24. „	17.9 „
„ „ „	37	144. „	22. „	15 2 „
„ „ „	38	163. „	27. „	16.5 „

is well exemplified in the leaf sheaths of Ruppia. It is stated by Goebel (1898, p. 556) that no general rule can be given for the time of stipular development, but that as Massart (1894) had already emphasized before him, they are formed and called into play when their function is most needed, as is in fact true of other parts of the leaf (Goebel, 1898, p. 503). I shall undertake presently to show why the leaf sheaths may be considered stipular as to their nature and origin.

In Ruppia the delicate parts in the region of the growing point are in great need of the protective offices of the early developed sheaths of surrounding leaves; and also the mature leaves, since they almost always contain axillary buds, require large enveloping sheaths. These considerations may explain the manner of sheath development.

d. Morphological and Morphogenetic Considerations.

The nearly related genus Potamogeton throws considerable light upon the question of the morphology and morphogeny of the leaf sheath. This genus, as is well known, embraces a great variety of forms, from those with broad floating leaves only (or with the addition merely of capillary phyllodia), passing through intermediate forms which have both narrow submerged leaves and broad floating leaves, to the typical submerged plants with narrow leaves only. In the last group we find basal sheaths on the leaves of most of its representatives, e. g. *P. filiformis, P. pectinatus, P. interruptus,* &c; but in the broad leaved forms and in the intermediates we find no sheaths, free stipules, however, being more or less prominent.

It seems clear, then, that in the submerged forms sheaths replace the stipules; and this deduction is borne out by such a species as *P. diversifolius*, which has the *submerged* leaves with stipules sometimes adnate, and even better by *P. spirillus*, where the stipules are always adnate to the submerged leaves, while those of the floating leaves in both species are free.

A comparison of any of the above mentioned typical submerged Potamogetons with Ruppia—especially *P. pectinatus* and *P. filiformis* —shows the similarity of the sheaths in the two genera. One may conclude, then that both the free stipules of the Potamogetons and the sheathing stipules of the submerged forms and of Ruppia are closely related, being connected as they are by many gradations; and it is probable that the sheathing stipule has been evolved from the free stipule, such as it is in Potamogeton.

As to the reason why this form of stipules is developed in water plants, the most obvious explanation seems to be that joined to

the leaf-base they can better perform their office of protection of the axillary structures. In the case of the grasses, where the sheath is also retained, Strasburger (1908, pp. 29, 30) states that besides protecting the soft lower part of the internodes when intercalary growth takes place, the sheaths also give the stem rigidity. Possibly this latter strengthening function applies also in some degree to the sheaths of water plants.

3. Axillary Scales.

a. General Characters and Anatomy.

In the axils of all the leaves are two small, ovate, scaly formations, one on each side of the median line of the leaf (Pl. III, fig. 8; Pl. VII, fig. 43, *a s*). These structures, common in water plants, and first shown by Irmisch (1858, p. 12) to be of general occurrence throughout the Potamogetonaceae, consist of generally two layers of cells rounded in cross-section, and loosely joined together, containing large nuclei and a large quantity of cytoplasm (Text-fig. 17). A longitudinal section of a single scale (Text-fig. 16), shows that

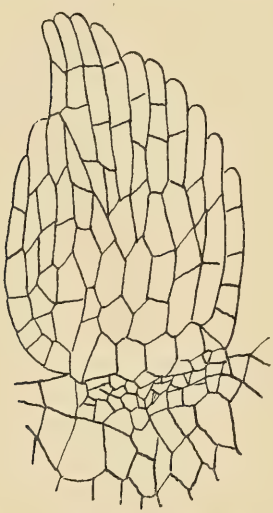

Figure 16.—Longitudinal section through axillary scale, showing arrangement and shape of cells. × 170.

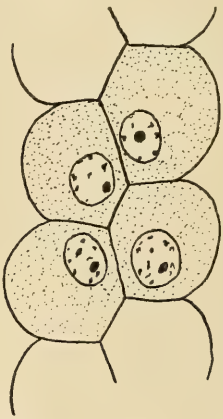

Figure 17.—Cells from cross section through axillary scale, showing cell structure. × 1400.

these cells are long and arranged more or less in rows in the upper part of the scale. Prillieux (1864) has found similar struc-

tures in *Althema filiformis*, which he erroneously believed to be stipules.

b. Function.

The nature of these "*squamulae intravaginales*" points to their serving the purpose of secreting organs. Schenck (1886, p. 9) is of the opinion that their secretion, which covers the growing point, is a protection against parasites, but of this point he is not certain. F. Müller (1877) had already claimed that the slimy secretions of such cells protected the delicate growing points from immediate contact with the surrounding water, a position which Schenck (1886, p. 10) criticizes by asserting that it is difficult to see how the outside water could injure the growing points. But Schilling (1894), who has made a special study of the subject, returns to Müller's view. He shows that the slime is impermeable to certain salts, &c. in solution in the water, and is probably only developed until the epidermal tissue and cuticle are far enough advanced to make such protection unnecessary.

Schilling's arguments are reasonable. The growing point is an extremely delicate part and might easily be injured by the salts or other substances in solution in the surrounding water. Especially is this true of Ruppia, a plant of salt or brackish waters. This would be an omnipresent danger to the young growing parts: the attacks from parasites would be intermittent or rare.

D. Subfloral Leaves

Although along the stem the leaves are distributed at fairly regular intervals, just below a flower they approach each other so closely as to appear opposite (Pl. VII, fig. 35; Text-fig. 18), a characteristic common to many other members of the family, notably Zannichellia, Althenia, Potamogeton, &c.

These two apparently opposite leaves, which I have designated the subfloral leaves, besides differing from the ordinary foliage leaves in their mode of arrangement, possess slightly specialized sheaths and considerably shorter leaf blades. The sheath of the outer or lower leaf envelopes that of the inner, while the sheath of the inner or upper leaf surrounds the peduncle, and both together form a protective envelope for the young flower before it elongates (Pl. II, fig. 6; Pl. VII, fig. 35). As a result of these conditions, the sheaths are slightly wider than those of the ordinary leaves, and they as well as the leaf blades are also shorter, the latter characteristic being in harmony with the bracteal nature of these leaves.

In all other respects, however—internal structure, axillary scales, &c.—the subfloral leaves are identical with the ordinary foliage leaves.

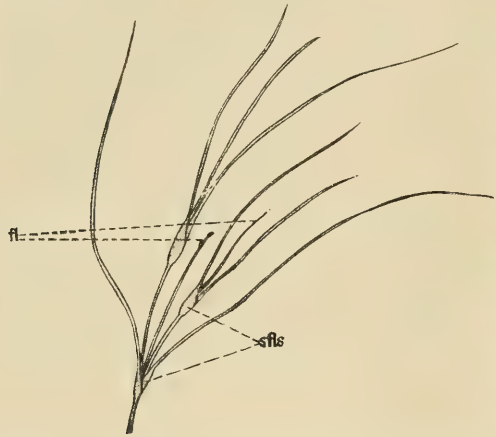

Figure 18.—Sketch of flowering branch, showing location of flowers and subfloral leaves. ½ natural size.

Koch and Irmisch have called these two leaves "folia floralia," an unwieldy term, whose English equivalent is at present applied to the modified leaves forming the floral envelope in the Phanerogams. On account of their position near the peduncle and their slight modification in form, they approach the category of "bracteal leaves" or "Hochblätter" of Strasburger (1908, p. 31) and Goebel (1898, p. 578), yet the difference from the ordinary leaves is so slight that such a classification seems unwarrantable. I have therefore adopted the term "subfloral leaves," although bearing in mind their approach to typical bracts.

E. Scale Leaves

Besides the subfloral leaves and ordinary foliage leaves, two other sorts of leaf structures occur in *Ruppia maritima,* quite similar in appearance and structure. These are very small membranous formations—one kind borne at the base of the ordinary branches and the other at the base of the floral axis (Pl. I, fig. 1; Pl. II, fig. 6, *vsl*; Text-figs. 19–20, *vsl* and *fsl*). The first sort is plainly what Goebel (1898, p. 572) has in mind when he writes of "Vorblätter." He says, "Die Vorblätter sind zunächst charakterisiert durch ihre Stellung. Wir finden sie—wo sie überhaupt vorkommen—bei den Dikotylen meist in Zweizahl an der Basis der Seitensprosse, bei den Monokotylen wird gewöhnlich ein Vorblatt angenommen, welches auf der dem Muttersprosse zugekehrten Seite des Tochtersprosses steht."

Strasburger (1908, p. 429) also mentions "Vorblätter," but with him they signify bracts or bracteal leaves. It is his category "Niederblätter" or "scale leaves" that includes the structures described by Goebel as "Vorblätter."

In accordance with the Bonn Textbook I have adopted the term scale leaf; the leaf at the base of the ordinary branch will be referred to as the vegetative scale leaf, while that at the base of the peduncle will be termed the floral scale leaf.

1. The Vegetative Scale Leaf.

a. General Characters.

This envelops the base of all axillary structures, except that in the axil of the upper subfloral leaf, and is developed on the side of the axillary member opposite to that of the subtending leaf. Flattened out, it is in the form of a long narrow triangle (Pl. VII, fig. 40), from 6 to 13 mm. in length; in position, its edges slightly overlap at the base, on the side nearest the subtending leaf (Text-figs. 19–20). If the axillary members are young, it completely envelops them; when they grow out, forming a branch, it remains sheathing the base of the branch.

b. Internal Structure.

Anatomically the vegetative scale leaf is composed of two layers of elongated large-vacuolate cells, rectangular in outline, with the nucleus flattened against the wall, and with a very few small chloroplasts. No vascular bundles are present. Pl. III, fig. 8 and Pl. VII, fig. 43, *vsl* show a transverse section, and Pl. VII, fig. 37 a surface view.

2. The Floral Scale Leaf.

a. General Characters and Structure.

The other form of scale leaf, which I have termed the floral scale leaf, occurs always at the base of the peduncle, on the side toward the youngest or upper subfloral leaf (pp. 97–98 and Text-fig. 20, *fsl*) and its base is coincident with the base of the floral axis for nearly one half of its circumference. Its development can be easily traced in Pl. IX, figs. 54, 55, 56, 51 and Pl. VII, Fig. 41, *fsl*, and it will be seen that never at any time does it completely envelop the floral axis, as does the scale leaf the base of the axillary shoot, but nevertheless partly surrounds it. When the peduncle elongates in the course of floral development, the floral scale leaf remains at its base, similarly as in the case of the vegetative scale leaf. Moreover, in its growth this scale leaf follows the growth of the flower and is entirely in independence of the adjacent axillary bud.[1] (Pl. VII, fig. 41, *fsl*).

[1] I have been unable to find a flower bud in which there was no branch in the axil of the upper subfloral leaf, which would of course, be an

In shape the floral scale leaf differs considerably from the vegetative scale leaf. It is shorter, almost symmetrically oblong and emarginate (Pl. VII, fig. 42; Text-fig. 19, *fsl*).

The internal structure is identical with that of the vegetative scale leaf.

3. Orientation of Scale Leaves in Floral Region.

The plan of a typical arrangement in the floral region is represented in Text-figs. 19–20. Here we find the members occurring in the following order, proceeding from right to left:—

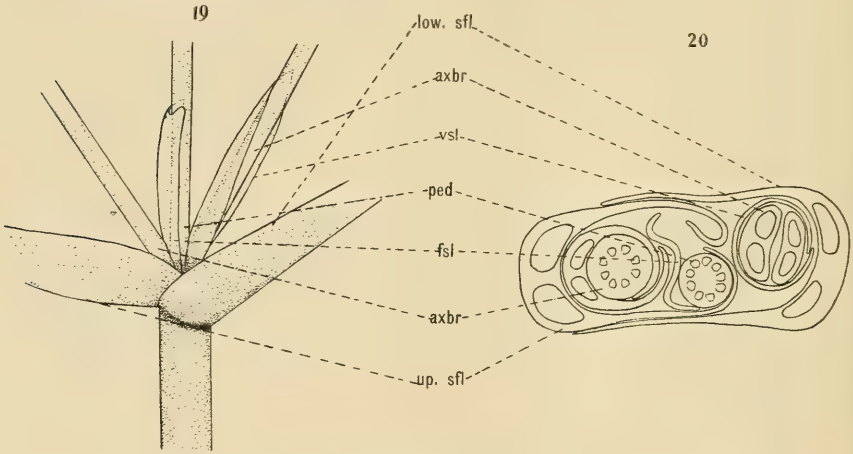

Figure 19.—Portion of the plant near the floral region, showing the two kinds of scale leaves and the subfloral leaves. The parts are somewhat separated so that they may be seen more clearly. *low. sfl.* lower subfloral leaf; *axbr*, axillary branch; *vsl*, vegetative scale leaf; *ped*, peduncle; *fsl*, floral scale leaf; *up. sfl*, upper subfloral leaf. × 6.

Figure 20.—Cross section through flower bud, below flowers, showing parts represented in figure 19. Abbreviations as in figure 19. × 35.

1. The lower subfloral leaf (*low, sfl*), sheathing the entire flower bud;
2. The branch (*axbr*), arising in the axil of this leaf;
3. The vegetative scale leaf (*vsl*), enveloping this axillary structure and borne at its base on the side furthest removed from the subtending subfloral leaf;
4. The peduncle (*ped*), bearing the flowers;

---

exception to the general rule. If such cases could be found, showing a normal floral scale leaf, this would prove that the scale leaf is borne on the peduncle and not on the axillary bract.

5. The floral scale leaf (*fsl*), adherent to the base of the peduncle in a position corresponding to that of the vegetative scale leaf;

6. The branch (*axbr*), arising in the axil of the upper subfloral leaf;

7. The upper subfloral leaf (*up. sfl*).[1]

4. Summary of Distinguishing Characters.

Irmisch (1851) has described the inflorescence in *Ruppia rostellata*. His account is in part as follows: "Die folia floralia bilden nun zwei Achseln, aus denen Zweige hervorbrechen, welche sich folgendermassen verhalten. Das erste tief an der Basis der Zweige stehende Blattgebilde ist eine dünnhäutige abgestutzte lanzettliche Schuppe, die sich um den Grund des Zweiges herumlegt. Ich will sie Vorblatt nennen. Es steht dasselbe, wie das auch sonst regelmässig der Fall ist, mit seiner Rückseite wegwärts vom Mutterblatte des Zweiges und dem Blütenstande A zugewendet";—and further, "Der Zweig in der Achsel des obern fol. flor. ist dem des untern in der äussern Bildung gleich."

In this and his description following, it is clearly evident that Irmisch considered the floral scale leaf and the vegetative scale leaf in an inflorescence to be identical, for he alludes to nothing but a vegetative scale leaf (Vorblatt) at the base of each branch. Of course it is possible that no floral scale leaf, as such, occurs in *Ruppia rostellata*, yet the two species are evidently quite similar. For example, Sauvageau (1891. II) finds no differences in the structure of their foliage leaves.

To sum up the differences between floral and vegetative scale leaves, they are in brief as follows.

1. Shape. The floral scale leaf differs markedly in shape from the vegetative scale leaf. A large number of specimens was examined and this difference was constant.

2. Position. As shown in Text-fig. 20, but more clearly were the section cut at a lower plane, the floral scale leaf does not envelop the axillary shoot as does the vegetative, but is turned toward and partially surrounds the young flower or the peduncle, according to the stage of floral development.

3. Development. The growth of the floral scale leaf is always correlated with the growth of the peduncle and flower—even when the axillary structure adjacent is as yet rudimentary. In case the

[1] The axillary scales have been purposely omitted. The cross section represented in Text-fig. 20 was cut above them.

floral axis is already well developed, one finds a correspondingly advanced development in the floral scale leaf, showing that it is now connected with and influenced by the flower and peduncle.

5. Morphological and Physiological Nature of Scale Leaves.

That the vegetative scale leaf is a leaf and not an axillary stipule, may be accepted without question, for its development occurs much later than that of the subtending leaf and its origin is from the axillary bud of the latter. As to whether one has to deal here with a degenerate leaf, or one that approximates the primitive form is a question difficult to settle without a definite knowledge of the primitive monocotyledonous leaf form. It is probable, however, that the ordinary foliage leaves are nearer to the primitive form. Moreover, the lack of vascular tissue and chlorophyll, and the simple structure in general indicate a degenerate form.

Whatever its genetic origin, the early development and complete enfolding of the young primordia, which later grow out beyond it, point to the present function of the vegetative scale leaf as being essentially protective.

The nature of the floral scale leaf is not so clear. The striking fact, however, that the branch adjacent to this scale leaf never has a vegetative scale leaf at its base would seem to point to the conclusion that the floral scale leaf is simply this vegetative scale leaf now connected with the flower and utilized for its protection in an embryonic state.

6. Comparison with Other Potamogetonaceae.

Scale leaves (préfeuilles) are found in Althenia (Prillieux, 1864) where there are often two on a branch below the first ordinary foliage leaf. They occur also in Zannichellia (Irmisch, 1858, p. 30) and Cymodocea (Bornet, 1864). In Potamogeton (Irmisch, 1858) the scale leaves are quite abundant, occurring on the rootstock as well as at the base of the shoots. The prophyllon, or fore-leaf, described by Holm (1905) in his writings on the grasses, is an homologous structure.

Root

A. General Characters

The roots in Ruppia, as in many submerged plants, are simple, and strikingly reduced in structure. The primary root, formed

in the embryo, does not persist; the sole representatives of the root system are small slender adventitious roots arising at the nodes (Pl. VII, fig. 36, *r*). These occur singly or rarely in pairs and are unbranched. Each root, in the early stages of its development, is surrounded by a sort of pocket formed from the secondary growth of the epidermis of the stem. After the root has broken through the tip of this pocket, the latter remains as a persistent sheath or collar at its base. A zone of root hairs appears on every root, developed from specialized piliferous cells (Textfig. 21, *rh*).

As to the length of the root, I have measured specimens 20 cm. long, but a much shorter length is the general rule.

The life of the root is comparatively short; for as the stem advances in its growth, new roots are successively put forth from new nodes, the older roots becoming gradually discolored and ultimately dead, together with the stem or rootstock whence they originate.

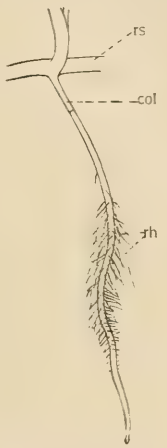

Figure 21.—Sketch of portion of rootstock and root; *col*, coleorrhiza; *rh*, root hairs; *rs*, rootstock. × about 1½.

B. Root Arrangement

Since the laws of the root arrangement in Ruppia are often obscure, as regards both the roots themselves and also their orientation with respect to the leaves, a somewhat more detailed description than that already given seems necessary.

Irmisch (1858, pp. 44–45) has described at some length the relation of root to leaf arrangement in *Ruppia rostellata*, and for a more detailed account I would refer to him. The following is to some extent a confirmation of his observations as referred to *Ruppia maritima.*

The root is developed at the node, at one side of the leafbase, and in the comparatively rare cases where a second root is developed at the same node (Pl. III, fig. 10), it assumes a corresponding position at the other side of the leaf base.

Since the roots, when occurring singly, invariably issue from the same side of the stem, and since their orientation with respect to the leaf of the node is as just stated, the following facts or laws of arrangement are established:—

1. The line connecting the points of insertion of the roots is straight, provided the stem has undergone no torsion (Text-fig. 22).

2. On account of the alternate arrangement of the leaves, the roots appear at successive nodes on opposite sides of the median longitudinal plane of the leaf,—i. e., if at one side of the leaf at any node, then at the other side of the leaf at the next higher or lower node (Text-fig. 22).

These simple rules of arrangement are, however, not often apparent. In a great many instances the stems to a considerable extent, due probably to currents of water, light conditions, &c., become twisted.

In such cases the orientat ionof the roots with regard to the leaves remains nevertheless constant, in accordance with the rule stated in (2). In other words, no matter what position the leaves may assume on the stem, the roots always emerge, in any two successive nodes, at one side of the leaf at one node, and at the other side of the leaf at the next node.

Compared with the other Potamogetonaceae, Ruppia has perhaps the simplest root system, if one considers the number of roots alone. Zannichellia (Campbell, 1897, p. 40), with generally two slender, unbranched rootlets at each node, and Althenia (Prillieux, 1864, p. 182) with two or sometimes more, borne on alternate nodes, most resemble it. The roots of Cymodocea (Bornet, 1864) are often borne singly, but differ in being branched. The roots of many Potamogetons (Irmisch, 1858) are more numerous, arising often in a circular line of insertion at the nodes. In Zostera (Grönland, 1851) and Phyllospadix (Dudley, 1893) a cluster of roots occurs at each node.

C. Anatomical Structure

1. The Coleorrhiza.

Extending for a distance of often 5 mm. on the root from its junction with the stem is a peculiar sheath-like structure, termed by Irmisch (1858) the "coleorrhiza" or root sheath (Pl. VII, fig. 38; Pl. VIII, fig. 45, Text-fig. 21). Beyond mentioning the fact that it occurs in *Potamogeton crispus, Zannichellia palustris* and *Ruppia rostellata*, Irmisch gives no description of it. In the related plants which Prillieux (1864), Magnus (1870), Schenck, (1886), Campbell (1897), and others describe, no mention is made of such a structure. Sauvageau (1889) indeed merely mentions a coleorrhiza as appearing in Zostera. Bornet (1864) notes in Cymodocea the formation of a

sheath "more or less short" at the base of the root, but does not give a detailed account of it, so that its nature is not entirely clear. This is, however, probably a coleorrhiza.

According to Sachs (1875, p. 143) in grasses and some other Phanerogams, the first root arises so deep in the interior of the embryonal substance that in the fully developed embryo of the ripe seed it is enclosed by a thick, sac-like layer of tissue, which is ruptured on germination and is known by the name of "root sheath (coleorrhiza)." Similar formations occur also in the first secondary roots of the germinating plants of *Allium cepa*, and occasionally elsewhere.

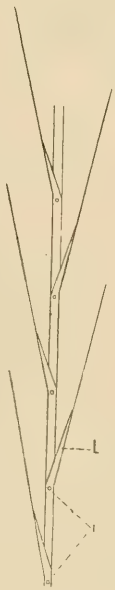

Figure 22.—Diagrammatic representation of root arrangement; *r*, root; *L*, leaf.

The coleorrhiza[1] in Ruppia, which is found on all the adventitious roots, is of entirely different nature. Its development can be observed at all the early stages of the growth of the root. The first indication of it appears during the origin of the young root within the stem. As the young root develops and appears in the stem cortex, a change in character takes place in certain of the epidermal cells of the stem, and in a few in the subepidermal layers, which lie in the region whence the root would naturally emerge. These cells become filled with protoplasm, their nuclei enlarge, and cell division takes place, the resulting cells being small and narrow (Pl. III, fig. 10; Pl. VI, fig. 31; Pl. VIII, fig. 44). In other words, a new growth starts up in the epidermis and a few of the cells of the subjacent layer, but principally in the epidermal cells. This stage is, of course, the most important for the proof of an entirely independent correlative origin of the coleorrhiza.

As the root grows out from the node, the epidermal or coleorrhizal cells divide by anticlinal walls, keeping pace with the root growth for some time, and forming the pocket or enveloping sheath already mentioned.

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[1] Since the term "root sheath" may be applied to several sorts of structures, it lacks definiteness. The subject of the present account, however, has a distinct character, as will be demonstrated more fully below, so that it seems fitting to apply the name coleorrhiza to it.

A cross section of the coleorrhiza as represented in Text-fig. 23 shows that it is composed principally of a single cell-layer. The section was cut purposely near the junction of root with stem, in order to show how toward the proximal end of the coleorrhiza a few of the cells of the subepidermal layer enter into its composition.

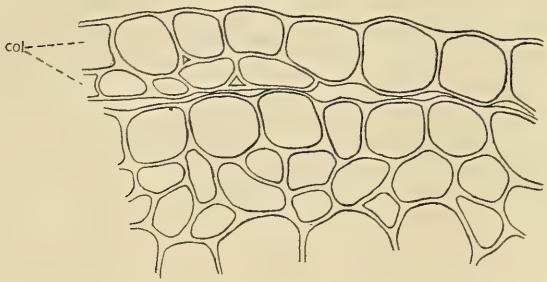


Figure 23.—Portion of cross section of root showing surrounding coleorrhizal layer. × 400.

As is shown by longitudinal sections, the cells in the outer or more distal region of this subjacent layer are undoubtedly the results of divisions similar to those which take place in the epidermal or coleorrhizal layer, but at the proximal or basal part of this subjacent layer the cells are larger and two or three rows deep, and those immediately adjacent to the root are considerably flattened. In this region, therefore, the subepidermal layers of the coleorrhiza are derived immediately from the cells of the stem without division, being forced outward by the development of the root and coleorrhiza.

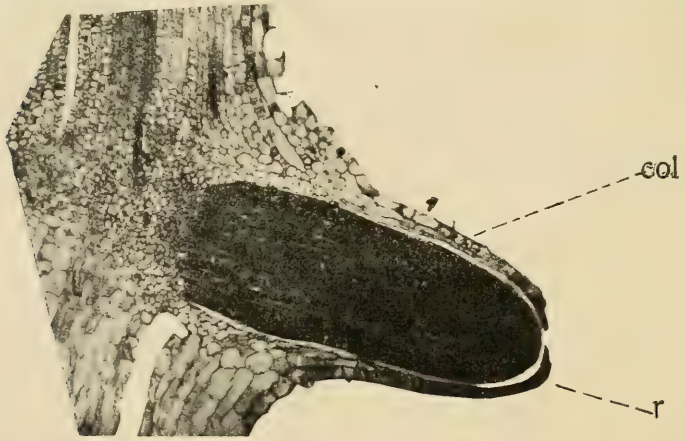


Figure 24.—Photomicrograph of longitudinal section of young root still enclosed in coleorrhiza; *col*, coleorrhiza; *r*, root. × 50.

Pl. VII, fig. 38 shows a well advanced stage, where by pressing with the cover glass the root was detached from its connection

with the stem and squeezed out of the coleorrhiza, producing the ruptured end of the latter. In this figure the coleorrhiza had attained approximately its maximum development. It then, with its enclosed root, appears to the naked eye as a small, smooth, blunt projection at the node. A photograph of a longitudinal section of this stage is shown in Text-fig. 24.

In the course of its growth the young root breaks through the coleorrhiza, which then remains at its base as a collar-like structure (Pl. VIII, fig. 45; Text-fig. 21).

An interesting incidental point in relation to the coleorrhiza, and one which indeed may be connected with its function, is the occurrence in its surface layer (when of more than one layer in thickness) of cells which are evidently secretion cells (Text-fig. 25).

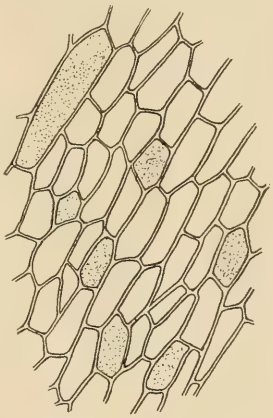


Figure 25.—Group of cells from surface of coleorrhiza, showing secretion cells. × 185.

It will be seen from the above description of the coleorrhiza in Ruppia that it is of entirely different nature from that to which Sachs (1875, l. c.) alludes. It has an external origin, being the outgrowth of the epidermis (including part of the immediately subjacent region) of that part of the stem which is situated over a developing root.

Such a structure as this evidently falls into the category of "correlative" growths. Having no immediate organic connection with the root and yet taking its inception close on the development of that organ, the nature of its growth is analogous, for example, to the correlative growth manifested in the development of fruit and fruit-covering after fertilization of the egg cell and during the development of the embryo.

As to the function of the coleorrhiza in Ruppia, not much can be said with any certainty. Perhaps it acts as an organ of protection for the root until the latter attains some length. The facts that it occurs only in water plants, so far as known; and that also, borne on it, are abundant secretion cells, may point to a functional secretion of slime of some sort to protect the young root in the water. Goebel (1893, pp. 233–237) has noted this quite general production of slime and slime-producing organs in water plants and has explained in some detail its beneficial effects. It has already been

noted that the axillary scales probably serve a similar purpose of protection for the young growing points of the stem.

The references in literature to a similar root sheath or coleorrhiza are scanty. As stated above, Irmisch gives it a mere mention in his work, as occurring in Potamogeton, Ruppia and Zannichellia. A similar formation in Lemna is described by Caldwell (1899). Long ago Strasburger (1873) noted and described an epidermal root sheath in Azolla. According to him the sheath was formed of two layers of cells, the inner layer eventually disorganizing and leaving the root free inside the sheath, which itself surrounded the root during its entire existence. Leavitt (1902), however, finds only one layer producing the sheath in Azolla, and through this the root soon pierces, leaving it as a collar at its base. Quite recently Lachmann (1906) has described an essentially similar structure in *Ceratopteris thalictroides*.[1]

2. The Growing Point of the Root.

Four meristematic layers appear well defined at the root tip (Pl. VI, fig. 31; Pl. VIII, fig. 44). The calyptrogen is a well marked region with several rows of tabular cells. The dermatogen layer, one cell thick, encloses all of the remainder of the meristematic tissue of the root. This dermatogen layer is continous, even at the apex. Inside of the dermatogen layer the periblem rows converge until they meet at the apex in a small cell area one or often two cells deep. At this same area the plerome originates, and the sides of the plerome cylinder are generally clearly marked off from the surrounding periblem.

Miss Daisy G. Scott (1906) in a recent paper has published the results of her investigations of the root tips of several aquatic monocotyledons. Among these are Ruppia, Naias and Zostera, in all of which the periblem and dermatogen arise from a single initial cell. These contain, then, according to Miss Scott, three apical meristematic regions, giving rise, the first to calyptrogen, the second to dermatogen and periblem together, and the last to plerome.

As will readily be seen, this arrangement disagrees with what I have described for Ruppia. Four meristematic regions are always clearly defined here. The dermatogen is invariably a continuous single layer, and the periblem arises quite often from a two-layered region at the apex, always showing at least one layer (Pl. VIII, fig. 44).

[1] Cf. also Goebel, 1898, pp. 469—470.

A four-layered type has indeed been known to be unusual since De Bary's (1884, p. 9) work, in which he describes it as appearing in only two plants, Pistia and Hydrocharis. Recently Campbell (1897, p. 40) has added Zannichellia to this list.

Beyond the papers of Miss Scott and Campbell, I find no record of other investigation on the apical meristem of the root tips of the Potamogetonaceae, if we except *Potamogeton crispus* and *natans*, studied by Treub (1876) and Flahault (1878), who assign to them three meristematic layers.

Considerable doubt and uncertainty have arisen concerning the tissue-forming capabilities of the various meristematic tissues of the growing point, a subject on which Scott (1894) has written an admirable resumé. Histogenesis in the roots of Ruppia is, however, perfectly clear. The plerome can be traced in its development into the central cylinder, communicating with the central cylinder of the stem. Thus, Pl. VIII, fig. 44 shows a plerome cylinder connecting

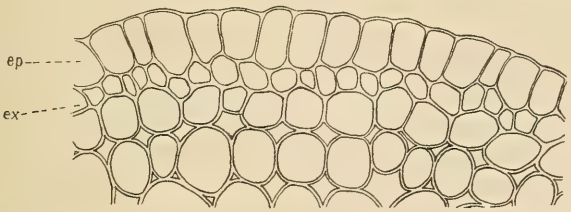


Figure 26.—Cells from outer part of cross section of root; *ep*, epidermis, *ex*, exodermis. Showing also two or three layers of cortex with intercellular spaces. ×325.

with the central cylinder of the stem. The width of this plerome at its base is about eight cells, which corresponds to the number of cells in the diameter of the central cylinder of the mature root—i. e., 7—10 (Pl. VIII, fig. 46).

3. The Anatomy of the Mature Root.

The internal structure of the root is even simpler than that of the stem. It consists of an epidermal region and a large zone of cortical parenchyma limited on the inside by the endodermis which surrounds the axial vascular bundle (Pl. VI, fig. 27). Each of these four parts will now be described in detail.

a. Epidermal Region.

The epidermis is a layer of large, thin-walled cells (Text-fig. 26), some of which produce the root hairs, to be described in detail presently. Beneath the epidermis, but not connected with it genetically,

is a layer of small, thick-walled cells, lacking intercellular spaces —evidently a strengthening layer (Text-fig. 26, *ex*). This may be designated the epidermoidal layer, as described by Juel (1884), or exodermis, as defined by Vines (1898, p. 111) and Strasburger (1908, p. 102).

(1) The Root Hairs. In a recent paper, Leavitt (1904) has published the results of his investigations on the root hairs of the higher plants, a subject which has hitherto been much neglected and concerning which only scattering references can be found here and there in the literature.

Leavitt has ascertained that the root hairs are of two types, depending on their manner of development. The first type may arise from any ordinary epidermal cell. The second type of trichome, common to most monocotyledons, arises from a specialized cell, which, in its embryonic state, Leavitt has termed a trichoblast.

It is to this second type that, as briefly noted by Leavitt, (1904, p. 292) *Ruppia maritima* belongs. According to my investigations, the root hairs arise here in the following manner. At a short distance back of the growing point, certain of the epidermal cells begin to differentiate. They are easily distinguished by their deeply staining, granular contents, and their larger nuclei, (Pl. VI, figs. 29, 32, 33). As to their size, there is some variation, but on the whole they are of about the same size as the ordinary epidermal cells. These peculiar cells are the primordia of the trichomes, called the trichoblasts, which by the subsequent development of tube-like projections from their free walls will produce the root hairs (Pl. IX, fig. 48).

As to their mode of origin, there seems to be no regularity. Often two or three non-piliferous cells alternate with the trichoblasts, but again, as many as a dozen or more ordinary cells may occur between two trichoblasts (Pl. VI, figs. 29, 32, 33).

Not all of the trichoblasts develop root hairs. They may remain simply as large cells with granular contents and large nuclei. They are evidently, then, as Leavitt has also noted, potential trichomes, the development of root hairs depending possibly on some stimulus. This explains why we find zones, often at considerable distances apart, where the hairs are developed in abundance.

A remarkable characteristic of the root hairs is their persistency. In roots which measured over 20 cm. in length, quite a number of hairs were noted still intact and apparently functioning even at the base of the root near the coleorrhiza. This condition is very common and may be due to the fact that the hairs are not worn off easily in the soft mud. Often, however, hairs do not

persist in this way—becoming broken off. Their basal parts then appear as blackened dead cells in the epidermis.

Leavitt (1904, p. 279) lays considerable stress on the small size in general of the trichoblasts and bases of trichomes as compared with the ordinary epidermal cells. In Ruppia, while some of the trichoblasts and bases of mature trichomes may occasionally be somewhat shorter, on the whole they average about the same size as the non-piliferous cells, even from the very first appearance of the trichoblasts (Pl. VI, figs. 29, 32, 33). In her paper on root hairs, Miss Snow (1905), from the study of several species, assigns no definite length to the hair-producing cells, but announces that in the same root the average length of the trichome-cells is less than that of the atrichomic cells.

b. Cortex.

Although to the cortex proper belong genetically the exodermis described above under the head of epidermal tissue, the cortical parenchyma, and the endodermis, I am describing each separately. Varying with the thickness of the root, from six to twelve concentric rings of large, rounded, thin-walled cells with diamond-shaped, schizogenous intercellular spaces, form the cortical parenchyma (Pl. VI, fig. 27). Often, in the mature root, on account of the radial expansion of the tissues, these parenchyma cells undergo a stretching, and separate from each other laterally, producing long strings of collapsed cells.

A longitudinal section proves that the intercellular spaces of the cortical parenchyma in the region of the endodermis, are often of a somewhat peculiar nature (Pl. VIII, fig. 47, *u*). These spaces arise by a local splitting of the wall, the split parts curving outward in opposite directions, forming openings which in the longitudinal section appear from spindle-shaped to circular in outline. These spaces may occur in series or singly at intervals. Near the endodermis they are small, increasing in size in the direction of the middle cortex. Before we come to the middle cortex, however, we find them elongated into long narrow canals, of which the diamond-shaped spaces described above are cross-sections.

c. Endodermis.

A single—occasionally, in places, double—ring of cells surrounding the vascular bundle, comprises the endodermis (Pl. VIII, fig. 46). Its radial walls show to a very slight degree the typical endodermal thickenings. The tangential walls are minutely wavy at irregular intervals. After treatment of cross-sections of the root with concentrated sulphuric acid, the endodermis as well as the epidermis and exodermis remain clearly defined.

d. Vascular System.

This is represented by a single vascular bundle in the center of the root, with a structure similar to that of the stem (Pl. VI, fig. 27; Pl. VIII, figs. 46, 47). No longer a typical radial root bundle, its present concentric structure admits of the same interpretation as regards adaptation as does the simplified bundle of the stem (see pp. 81–82). It differs from the stem bundle in only a few minor details. Barely as large as that of the stem, in all cases observed the root bundle retains intact the axial vascular area composed of a few tracheae. These tracheae are peculiar in that they possess no thickenings of any sort. Their walls, although extremely thin, can be distinctly seen in cross and longitudinal sections (Pl. VIII, figs. 46, 47, *tra*). Schenck has observed a similar peculiarity in the root of *Potamogeton densus*. He says (1886, p. 61), "Die Gefäße aber erfahren keine deutliche Differenzierung der Wandung; auf Längsschnitten sieht man keine Verdickungen oder nur schwache Spuren, so daß die Gefäße als Gänge erscheinen. Überhaupt erfahren in den Wurzeln der monocotylen submersen Gewächse die Gefäße, obwohl sie überall sofort zu erkennen sind, keine weitgehende Ausbildung. Die Resorption der Querwände tritt meist ein, bevor Verdickungen angelegt werden."

Five or six sieve tubes, with their companion cells, are situated at more or less regular intervals just inside the endodermis, forming an irregular ring. These can be distinguished in cross-section by their generally larger, nearly empty cell-cavities, their position just inside the endodermis, and their accompanying companion cells. In longitudinal section the sieve plates may be seen, as also the accompanying companion cells with their protoplasmic contents (Pl. VIII, figs. 46, 47 *s*).

The remaining tissue of the bundle is parenchymatous, and on account of its disposition in all parts of the bundle, it is impossible to distinguish phloem and xylem parenchyma. It may therefore be termed "connecting tissue" in accordance with Van Tieghem's (1870–71) "tissu conjonctif" or Schenck's "Verbindungsgewebe" (1886, p. 59).

e. Brief Comparative Study of Roots of Other Potamogetonaceae.

In general, *Potamogeton pectinatus* and *Zannichellia palustris* agree with Ruppia in the vascular structure of their roots. The main difference is the presence of only one central trachea, which is considerably enlarged (Schenck, 1886, p. 61, figs. 80, 81). I find no reference in the literature to the cortex or epidermis of these plants, but see no reason why it should differ to any extent from that of Ruppia. Very probably also other slender sub-

merged Potamogetons, such as *P. filiformis*, have a similar root structure.

Another plant, whose roots resemble closely in internal structure those of Ruppia, is *Althenia filiformis*. Epidermis, exodermis and cortex are practically identical with the same tissues in Ruppia, and although Prillieux's (1864) description and figures of the bundle leave much to be desired, there is evidently a strong resemblance to Ruppia.

The structure of the mature root of Cymodocea apparently differs entirely from our plant, most certainly in the composition of the central cylinder, according to Bornet's (1864) description and figure.

D. Functions of the Root

As is well known, the two main functions of the root are—1. to absorb water and watery solutions from the soil, and 2. to act as organs of attachment. That these functions are both of much importance in the roots of land plants is an established fact; that their relative importance assumes the same proportions in submerged plants is not so well established.

Some authorities, such as Sachs (1887) and Vines (1898), have expressed the view that the roots of submerged plants are used mainly as organs of attachment. Schenck (1886, pp. 57, 58) modifies this somewhat, concluding that the absorption is of not much importance, but may possibly supply mineral solutions from the soil.

Strasburger's (1891) view, as expressed in his work "Über den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen," is similar to Schenck's. In the Bonn Textbook (1908, p. 165), however, Noll says, "Wasserpflanzen .... vermögen Wasser und gelöste Stoffe überall an ihrer Oberfläche aufzunehmen. .... Die in den Boden eindringenden Wurzeln vieler submersen Pflanzen tragen aber zur Ernährung und zum Gedeihen dieser Wasserpflanzen wesentlich bei"—thus laying considerable emphasis on the absorptive power of the root.

Pond (1905) has indeed recently proved quite conclusively that this absorption is of more importance than was formerly supposed—to such a degree that, for example, in *Ranunculus aquatilis trichophyllus,* one of the various submerged plants he has experimented upon, specimens rooted in soil exceeded in growth those rooted in clean washed sand 62.96%. Similar results were obtained by him with other submerged plants.

Not only the evident carefulness with which he has conducted his experiments, but also the variety of species and number of specimens used, joined with his very positive results, should put at rest all doubt as to the importance of the absorptive rôle of the roots of submerged plants.

On the other hand, Pond's experiments fail to show conclusively whether or not water and dissolved salts are absorbed by the part of the plant above the soil—a condition which is indicated by the reduction of the xylem area of the root.

Too much emphasis, therefore, must not be laid upon the absorbing capacity of the root, as is shown by the following considerations:—1. the absence of transpiration as we are acquainted with it in land plants; 2. the probable absorption by the parts of the plant above the soil of nutrient solutions from the surrounding water; 3. connected with these two conditions a reduction of the xylem area to a few tracheae of rudimentary nature; and 4. the total lack of branches and the slenderness of the roots.

In brief, the absorption carried on by the roots of submerged plants and the importance of this function in the economy of the plant is much greater than is implied by Schenck, as the experiments of Pond demonstrate; but, on account of the peculiar environmental conditions of submerged plants, it can never equal in importance the absorption of the roots of land plants.

THE ECOLOGY OF THE VEGETATIVE ORGANS

Introductory

In view of the fact that Ruppia is a submerged plant, living under water at all seasons of the year, and unable to live out of it, a study of the methods by which it accommodates itself to this life is of interest, especially when one compares it with a typical land plant.

Of course, in a comparison of these two types, the one point of vital importance to be noted first of all is the radical difference in the nature of their environment: the land plant pushes its stem and leaves into the air, a gaseous medium; while the submerged plant extends its shoots entirely surrounded by water, a liquid medium.

The striking formal, structural, and physiological dissimilarities which obtain between land and submerged plants have their fundamental origin in the physical differences of these two media and the concomitant variations in quality and intensity of light, temperature, &c. These physical factors have already been clearly stated by Warming (1902, pp. 127 ff.), Schimper (1898), and others, so that it is unnecessary to recount them here.

On account of the various methods of ecological classification by different authors, the assignment of Ruppia to a definite ecological group is not as easy as might seem at first sight. Among his four ecological groups Warming (1902, p. 121) defines the hydrophytes as being those plants that are surrounded wholly or for the most part by water, and those that grow in very moist earth. Of the subdivisions of this group the "Enalid society or sea grass vegetation" includes such plants as Zostera, Cymodocea, Phyllospadix, Potamogeton, Althenia, Ruppia, &c. (l. c. p. 156).

More recently, however, a tendency has been manifested to restrict the term hydrophytes to plants of fresh water only (e. g. Atkinson, 1905, p. 484). According to this view Ruppia is excluded and must be classified as a halophyte, an arrangement which seems reasonable, if one accepts the literal meaning of the term "halophyte."

As a matter of fact, a study of the plant shows that the great majority of its adaptive characters fit it for membership in the hydrophytes, and only a few—possibly not more than one or two —features added to its hydrophytic characters would qualify it for

a halophyte. And when one reviews the strikingly diverse characters exhibited by plants living in salty soil—which is the vegetation one naturally thinks of as halophytic—and by those living in salt water, it seems best to avail ourselves of Schimper's (1898, p. 817) terms "land halophyte" and "water halophyte" as a solution of the difficulty.

Considered as a water halophyte, therefore, Ruppia has both hydrophytic and halophytic adaptations. I shall outline first the former, taking up in order those modifications that occur in the shoot and in the root, and secondly describe the halophytic adaptations.

Hydrophytic Adaptations

A. The Shoot

1. Gross Morphological Adaptations.

In its external form and style of branching the stem of Ruppia presents a marked contrast to the stem of a typical land plant. Since water has such a greater density than air, it becomes no longer essential for the plant to have a stout, firm axis capable of holding itself erect and supporting numerous branches. Instead we find the stems of Ruppia long and slim, and except at the very apex, of equal diameter throughout. For the same reason the branches are similar, and as long or longer than the principal axis from which they arise. Hence the peculiar wide-spreading branch system which I have already described—a type impossible in a land plant without a copious development of strengthening tissue.

The leaves of Ruppia, arising from such a weak, slender stem, are of enormous length compared with the leaves of an ordinary land plant having a main axis of similar diameter. This extreme length is again made possible by the greater density of the surrounding medium. A leaf of similar proportions in a land plant would have great difficulty in holding itself out in a plane suitable for receiving the rays of light.

The advantages of this extreme length seem quite apparent. Coupled with the narrowness of the leaf, the effect is just as in aquatics with finely divided leaves, such as Batrachium, Ceratophyllum, &c., i. e., to present a large amount of surface to the water in proportion to the volume of the leaf. This increase in leaf surface is beneficial for several reasons. In all probability much of the nutrient mineral solution requisite for metabolism is absorbed by water plants directly from the surrounding water. Moreover,

both oxygen and carbon dioxide are necessary for the life of the water plant just as in the case of the land plant. Of the gases in solution in water, both oxygen and carbon dioxide are present, indeed, in a greater proportion than in air. The diffusion of these gases, however, takes place much more slowly than in the air, so that the larger the area of leaf surface, the more readily will the requisite amount of gases be absorbed (Warming, 1902, p. 127 and Goebel, 1893, pp. 248 ff.).

It is obvious, therefore, that for the purpose of carrying on its absorption both of gases and nutrient mineral solutions in the best manner possible, the long, slender leaf of Ruppia is an ideal form.

In the salt-marsh creeks and ditches where it makes its home, Ruppia is constantly subjected to the action of fairly strong tidal currents. On this account also it is advantageous to the plant to have slender leaves; for such easily accommodate themselves to these alternately inflowing and outflowing tidal currents. This accommodation becomes the easier from the fact that the leaves are not dorsiventral, but alike on both flat surfaces and, therefore, bisymmetrical; a condition which may be referred to the diffuseness of the light in the water, as well as the constant moving about of the leaves, resulting in a tendency to equality of conditions on both sides of the leaf.

A condition of general ecological significance, which affects all of the vegetative organs, but particularly the shoot system, has to do with the tidal currents mentioned above. At times these currents are even so strong as to detach portions of plants, which I have often observed floating up or down stream, according to the tide. These plant segments become entangled in grass, &c. along the stream edge, or collect in some miniature cove and then begin an independent existence, at perhaps a considerable distance from the parent plant. This is probably a common mode of vegetative reproduction among such water plants.

2. Internal Structural Adaptations.

a. Epidermal modifications.

In many respects the epidermis of stem and leaf clearly reflects environmental influence.

In contrast to the thick outer or free walls of the epidermal cells of land plants, we meet here with a thin wall. Surrounded by water, there is no danger of the drying up of the plant by evaporation from the epidermal cells—a process which, on the other hand, commences immediately on exposure of the plants to the air—and consequently a thick wall would here be superfluous. The fact that even in Ruppia the outer wall of the epidermal cell is slightly

thicker than the others, may possibly be attributed to the necessity for some slight degree of firmness in the covering of the shoot.

Besides the thinness of the walls, the epidermis of the leaf exhibits the following two remarkable peculiarities, which have already been observed in similar aquatics by Warming (1902), Schenck (1886), Goebel (1893) and others, and need not, therefore, be entered into in detail here.

The light is weakened to such an extent by reflection on the surface of the water, absorption in the water, &c., that most of the chloroplasts, for the purpose of the best illumination possible, are located in the epidermal cells, which therefore assume the rôle of photosynthesis, but yet have not at all the shape of the palisade cells of land plants.

As in the majority of other submerged plants, no stomata occur in Ruppia, nor, as already ascertained by Sauvageau (1891, II, p. 209) any of the apical leaf pores found by him in other water plants, so that openings of any kind are lacking in the epidermal covering. The reasons for this, dependent on the characteristic mode of food absorption, the lack of a transpiration current as it occurs in land plants, the extreme permeability of the leaves of aquatic plants to gases, &c., have been fully elaborated by the authorities quoted above (Schenck, 1886 and Goebel, 1893) and need not be dwelt upon here.

It seems to be generally admitted that where stomata do occur in submerged species, they are to be looked upon as hereditary structures, rather than as possessing any ecological significance.

Schenck (1886, p. 6) claims that stomata in submerged leaves are positively harmful, admitting the water into the air reservoirs located in the lacunae. Sauvageau (1891, II), although admitting their uselessness, maintains that they are not harmful to the plant. They have gradually disappeared from the leaves of water plants, not because they are harmful, but because they are useless.

Development of slime. The slime developed by the axillary scales in the shoot has been already treated in detail. It is of ecological significance in that a protection is thus effected for the delicate growing points against their aquatic environment, the protective function of slime being well known (cf. Goebel, 1893, pp. 232–237).

b. Development of Air Spaces.

The formation of large and small intercellular air spaces, most pronounced in stem and leaves, is one of the most striking histological characters of the shoot system. In general, the larger of these air spaces, such as the zone occurring in the stem, and the two

longitudinal rows present in the leaves, receive the special name "lacunae."

The function of these lacunae has not yet been sufficiently investigated. So far as is known, they occur in all water plants. Schenck (1886, p. 49) states that water plants grown on land diminish the size of their air spaces and, conversely, land plants grown under water reveal a tendency toward a loosening up of the cortical parenchyma. This necessarily indicates that the formation of air spaces is in some way connected with and necessitated by an aquatic environment. Haberlandt (1896) has probably hit the truth of the matter when he explains that this is a method of obviating the difficulty of osmotic interchange of gases in submerged plants: "Es wird eine "innere Atmosphäre" geschaffen, mit welcher die geschiedenen Gewebe einen lebhaften Assimilations- und Atmungsgaswechsel unterhalten." The larger these inner air reservoirs are, so much less will the plants have to suffer the difficulties of direct interchange of gases with the surrounding water. It is probable also that the considerable amount of air and gases enclosed in these intercellular spaces is of advantage for submerged as well as for floating plants, by its lessening of the specific gravity of the plant.

c. Absence of Mechanical Tissue.

As has been, in part, pointed out above (see p. 116), a land plant with dimensions of stem, branches and leaves similar to those occurring in Ruppia, must of necessity develop considerable mechanical tissue. But in no part of the vegetative organs of Ruppia is a characteristic thick-walled tissue developed. That such mechanical tissue is entirely absent is to be explained in the greater supporting capacity of water as compared with air, resulting from the greater density of the aqueous medium. In this way this lack of supporting tissue is to be considered as an adaptation to environment.

d. Reduction of the Vascular System.

The vascular system is greatly reduced. If we except the minute cortical bundles of the stem and the small lateral leaf nerves, the entire vascular system of the shoot is represented by a single axial vascular strand. The xylem portion mostly disappears in the mature stages except at the nodal regions, leaving a central cavity in the vascular area. The phloem portion is, however, in all cases intact, consisting of sieve tubes, companion cells and phloem parenchyma.

One may lay this vascular reduction entirely to the different mode of nutrition employed by submerged plants. On the one hand, the food solutions formerly conveyed from the roots by way of the stem are probably now absorbed in large part from the surrounding water,

and on the other hand, the transpiration current, unaided in its work by stomata or even by apical leaf pores, and, moreover, rendered unnecessary by the presence of water on all sides, must inevitably be diminished.

That the sieve tubes and their companion cells should remain intact simultaneously with a complete degeneration of the xylem, seems reasonable when we consider that the function of the phloem is the transportation of *elaborated* food.

In another respect the reduction of the vascular system is of ecological importance; for not only are the vascular elements reduced quantitatively, but also the fact that practically all of the vascular system is concentrated into a single bundle, which is axial, deserves especial note.

That this axial position of the bundle in the stem is considered to have been attained phylogenetically, through a gradual displacement of the more peripheral bundles toward the center of the stem and fusion there into a single concentrically arranged bundle, has already been touched upon in the account of the morphology of the stem (p. 81–82).

Ecologically considered, this axial arrangement enables the plants to bend about easily and accommodate themselves to the movements and currents of water. For the axial bundle of the stem, with its slightly thickened endodermis enclosing the long cells of the vascular tissue, is naturally the region most resistant to bending movements. Now, it may easily be seen that a plant with its vascular area in such a position is capable of bending much more readily than one in which this area is more or less peripheral, as in the typical land plant. Such an arrangement is analogous to the axial strand of roots, and there subserves a similar purpose.

B. The Root

1. Gross Morphological Adaptations.

Another result of the absorption of nutrient solutions by the shoot system directly from the surrounding medium is the great reduction of the root system. This consists entirely of slender, unbranched, adventitious roots arising singly at each node of the creeping stem —a simplicity of form and development which is correlated with the function of the root, and which has been already discussed in detail under the morphology of the root (pp. 103–114).

As has already been pointed out, the development of a coleorrhiza or root sheath may have some bearing on the environment, protecting

the root in its very young stages. It may be here again noted (cf. p. 107) that possibly the soil or the water, containing common salt in solution, would injure the very young root if not thus protected.

2. Internal Structural Adaptations.

a. Air Spaces.

The root cortex, as is the case in the shoot, shows many intercellular spaces, but much smaller. These, however, are often made larger by the collapsing of the cells. The function of these air spaces may probably be explained in the same way as in the shoot (p. 119).

b. Reduction of the Vascular System.

The vascular bundle of the root, of essentially the same structure as that of the stem, admits of the same interpretation, as regards the reduction of its elements, as in the stem. Especially significant is the reduction in this case, however, since the root is properly the absorbing organ of an ordinary plant, and as such should possess at all events a well developed vascular system. The absence of such a one here is the most conclusive proof of the comparative small amount of absorption carried on by the root system.

In this connection the presence of thin-walled tracheal cells without thickenings, still intact in the xylem area of the bundle, is interesting in comparison with the axial canal caused by their dissolution in the stem. Their presence may indicate a need for them in the root, and therefore some degree of absorption by this organ.

Halophytic Adaptations

A. General

It was pointed out by Schimper (1890, p. 1047, and 1891, pp. 25 ff.) that any considerable amount of salt in the cell sap is detrimental to the plant, and that here we have the probable cause of the characteristic halophytic modifications, which aim, therefore, at a lessening of the transpiration current. To this Warming (1902, p. 309, 310) replied that even if transpiration were diminished to a very low degree, slowly but surely an amount of salt would be collected in the plant which would eventually prove fatal. On the other hand, Warming saw better logic in another idea of Schimper (1890), which has become the widely accepted view at the present time—namely, that the protective contrivances against strong transpiration are necessary in halophytes, because absorption of water from a salt solution is slow and difficult.

On account of this difficulty in water absorption, then, one finds exhibited in land halophytes many water-storing devices and typical xerophytic methods of diminishing transpiration.

The water halophytes, on the contrary, especially the submerged aquatics, such as Ruppia, Zostera, Phyllospadix, &c.—members of the Enalid hydrophytic society of Warming (1902, p. 156) as above noted—evince none of these modifications. The hydrophytic adaptations already described for Ruppia show how closely this plant resembles a typical submerged fresh water hydrophyte. Although surrounded by salt water to a much greater extent than land halophytes, yet it shows none of the characteristic xerophytic modifications which are associated with land halophytes in general.

The explanation of this may be based on the fact that transpiration, as such, does not appear in Ruppia. The comparatively small amount of water absorbed by the roots, the absence of any openings in the leaf through which water could pass, such as Sauvageau (1891, II, pp. 127 ff.) has described for Zostera, Phyllospadix, Halodule and Potamogeton; moreover, the fact that the epidermal cells of the leaf, with the exception of the secretion cells, are all photosynthetic and absorb solutions from the outside into the interior, indicate the giving off of a very small amount of water, if any from the leaves. Waste gases, however, can easily pass out through the cell walls in solution. On account of these conditions, structures adapted to the retention of a supply of water and reduction of transpiration, are unnecessary, and we accordingly find an absolute lack of such halophytic adaptations in Ruppia.

B. The Adaptation to a Salt Water Environment

In one particular, however, Ruppia shows a distinct halophytic adaptation. This is exhibited in its power to withstand the plasmolytic action of salt water. Ganong (1903) has found that the root hairs of certain land halophytes possess specific abilities to resist plasmolysis in various solutions of sea water, showing in this way a greater or less halophytic adaptation. He says (1903, pp. 353, 354), "I found a close correspondence between the halophilism of a plant and the power of its root hairs to resist plasmolysis. This power has of course been gradually acquired, but what its physical basis is I do not know; though we shall probably find that substances osmotically equivalent to the salt of the sea water have been formed in the sap of the hairs."

But Ruppia, and all of the allied salt water genera, such as Zostera, Phyllospadix, &c., show an even greater adaptation than

these land halophytes, since they live and flourish entirely in a salt-water medium.

Wishing to ascertain how great a concentration of salt water *Ruppia* would stand without plasmolyzing, I tried first a 105 per cent solution, obtained by evaporating salt water (taken at high tide at Savin Rock, near the entrance to New Haven Harbor), to the desired concentration. As is indicated in the following table, (p. 125), both leaves and root hairs showed occasionally a very slight plasmolysis. In the root hairs, indeed, the protoplasmic movement continued, although in most cases the ends of the hairs, especially, showed a slight plasmolysis. A solution of 110 per cent strength, however, prepared in the same way, produced a marked plasmolysis in both leaves and root hairs.

In order to get a comparison with submerged fresh water plants, I experimented with the leaves and root hairs of Elodea and Callitriche, with the results as shown in the table (p. 125).

Compared with Ganong's results, a few of which also are given in the table, my experiments show that the plasmolysis index in Elodea and Callitriche is about equal to that of Atriplex and Hordeum, so that there is very little halophytic adaptation in this respect in the latter plants. This is to be expected, since Ganong (1903, pp. 359, 360, 364) expressly states that these grow in the higher and drier places of the salt marsh.

Another point illustrated by the experiments with Elodea and Callitriche is the slightly greater resistance in both cases of leaves as compared with root hairs. This is hardly to be looked for, since it would naturally be supposed that the roots would be accustomed to somewhat stronger solutions in the soil and would therefore evince a greater resistance to the plasmolyzing action.

Elodea, as is natural, being a very delicate plant, is more sensitive in both cases than Callitriche.

Being curious to know how much pure salt (sodium chloride) Ruppia would stand, I used solutions of 2.5, 3, and 5 per cent with the following results.

1. Leaves of *R. maritima*, placed in 2.5 % NaCl solution, did not plasmolyze.
2. „ „ „ „ „ „ 3 % „ „ plasmolyzed in 4–5 min.
3. „ „ „ „ „ „ 5 % „ „ „ in about 1 „

Since ocean water in general is known to contain about 3.5 per cent of salts (Atkinson, 1905, p. 622), it would seem from the above that Ruppia could not live in it. And yet, as the table (p. 125) shows, Ruppia does not plasmolyze in the salt water of New

Haven Harbor, and not often even in a 105 per cent strength solution of this.

This would lead one to conclude *a priori* that the water of New Haven Harbor does not contain as much salts as the 3 per cent quantity of NaCl of the above experiment, and certainly not as much as the 3.5 per cent of ordinary ocean water.

On next ascertaining the percentage of salts contained in the water of New Haven Harbor (procured, as in the first experiment, from Savin Rock, near the entrance to the Harbor, at high tide), I found by evaporation that the proportion was about 2.8 per cent, as would be expected from the *a priori* conclusion. This amount, therefore, explains why Ruppia plasmolyzed in a 3 per cent salt solution, but did not plasmolyze in the water of New Haven Harbor.

The sea water used, although purposely obtained at the entrance to the harbor and at high tide, is, therefore, quite brackish. The fact that Long Island Sound is considerably shut off from the ocean and also has several large rivers emptying into it, probably accounts for this. Very probably a similar percentage of salts prevails all along the Connecticut coast.

It is possible that the sea water used in Ganong's experiments had a greater content of salt. If so, his results with Atriplex and Hordeum mean somewhat more than the comparison in the table indicates.

An interesting point which should not be overlooked, since it shows how delicately adjusted these plants are, comes to light in the sometimes slight plasmolysis of Ruppia in the 105 per cent solution. A little calculation shows that this is about identical in strength with the 3 per cent salt solution, at which plasmolysis occurs very slowly. It is perfectly clear, then, that Ruppia is adapted to life in water containing a solution of sodium chloride and other salts; that this solution does not equal in strength that of the ocean in general and hence may be termed brackish; and furthermore, that Ruppia could not live in such ocean water; that this adaptation of the plant is brought about through an ability to resist plasmolysis by maintaining in some way a higher osmotic tension than prevails in submerged fresh water plants, probably by the presence of an equalizing salt solution in the cells themselves.

RELATIVE RESISTANCE TO PLASMOLYSIS.

Percentage of Sea-water	LEAF (epidermal cells)			ROOT (root hairs)			Comparison with Results of Prof. Ganong on Root Hairs of Land Halophytes[1]				
	Elodea canadensis	Calli-triche palustris	Ruppia maritima	Elodea canadensis	Calli-triche palustris	Ruppia maritima	Salicornia herbacea	Suaeda maritima	Plantago maritima	Atriplex patulum	Hordeum jubatum
10	—	—	—	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—	—	—
30	—	—	—	—	—	—	—	—	—	—	—
40	—	—	—	very slight	—	—	—	—	—	—	—
50	very gradual appearing in about 7 min.			gradual, but finally marked	gradual					plasmolysis	plas-mo-lysis
60	bet. 40 s. & 2 m.	very gradual 7—9 m.	—	rather gradual but finally marked	rather gradual	—	—	—			
70	35—75 s.	45 s.—2½ m.	—	1 min.	distinct	—	—	—	plasmo-lysis		
80	12—15 s.	45 s.–3 m.	—	1 m.	—	—	—	plas-molysis			
90	10 s. & under	25 s.—1¼ m.	—	30 s.	—	—	—				
100	immediate	15—45 s.	–	20 s.		–	plas-molysis				
105	immediate	im-mediate	occasion-ally very slight	immediate		occasionally very slight					
110	immediate	im-mediate	distinct and fairly rapid	immediate	–	rather slow but finally distinct					

[1] Ganong, in all cases, gives the solution which the plant will "endure without plasmolysis." I assume, therefore, that plasmolysis would occur at the next higher strength of solution.

Adaptation and Heredity

When one reviews the manifold ways in which Ruppia is adapted to its environment, it becomes clear that this plant represents an advanced stage of special evolution, resulting in a particular type of plant, growing entirely below the surface of the water and almost ideally adapted to the novel conditions which present themselves.

That the characters of aquatic plants cannot, however, always be explained on the hypothesis of adaptation, Sauvageau has well illustrated. Another factor should be reckoned with, namely, heredity. For instance, among other examples, Sauvageau (1891, II, p. 121) speaks of *Althenia filiformis* and *A. Barrandonii*, which grow side by side in certain ponds near Montpellier: "Les feuilles de la première ne possèdent jamais d'éléments épaissis; celles de la seconde, au contraire, ont non seulement leur unique nervure entourée d'un endoderme puissant, mais l'épiderme a ses parois plus épaisses, le limbe est parcouru par deux gros cordons fibreux plus ou moins lignifiés, et la gaine en montre plusieurs semblables. Ces faits sont complètement inexplicables si l'on admet l'action prédominante et quasi exclusive du milieu."

It is evident that as Schenck (1886, p. 7) has declared, adaptation and heredity are two opposing factors in the transformation of an organism, and that "l'état anatomique . . . . maintenant dépend assurément non seulement du temps depuis lequel l'adaptation a commencé, mais aussi de leur structure originelle et de leur résistance spécifique à l'adaptation, autrement dit, des caractères qui leur ont été légués par hérédité." (Sauvageau, 1891, II, p. 120.)

One meets in Ruppia very few of these useless structures handed down presumably from former generations. We have seen that the cortical bundles of the stem are evidently rudimentary structures, but one cannot affirm with certainty that they are now useless. Again, the tracheae of the axial bundle in the shoot become so disorganized in the mature condition that it would seem as if here were an ancestral structure which is no longer needed. And, as if to carry out this idea, we find the tracheae absolutely lacking in such highly adapted plants as Ceratophyllum and Naias (Schenck, 1886, p. 30).

Summary

1. It is best to classify Ruppia ecologically as a water halophyte. As such it exhibits both hydrophytic and halophytic adaptations.

2. The hydrophytic adaptations of the shoot are as follows: first, in its external form it shows a weak, wide spreading branch system, with slender stems and long grass-like leaves; second, in its internal structure, it reveals a thin-walled epidermis, photosynthetic and without stomata, in the leaves, a production of slime by the axillary scales for protective purposes, a copious internal development of air spaces, a complete lack of mechanical tissue and a reduction of the vascular system to a single main axial bundle and two small lateral bundles in both stem and leaf.

3. The hydrophytic adaptations of the root are as follows: first, in its external form, a reduction of the root system to small, unbranched, adventitious roots, borne singly at the nodes, and the formation of a protective coleorrhiza; second, in its internal structure, the presence of numerous air spaces and the reduction of the vascular system to a single, axial, concentrically arranged bundle similar to that in the shoot.

4. The characteristic adaptations of land halophytes are wanting here, for the reason that their cause, the need for reduction of transpiration, is lacking.

5. Ruppia shows, however, a remarkably interesting halophytic adaptation in its power to live in salt water, which, when applied to submerged fresh water plants, causes instant plasmolysis.

6. This salt water is not equal in strength to that of the open ocean, containing in New Haven Harbor, about 2.8 per cent of salt, and may therefore be termed "brackish".

7. My experiments show also that this power is confined to a very slight margin, i. e., that slightly concentrated harbor water causes plasmolysis in both root hairs and leaf cells of Ruppia proving that the plant, as now constituted, could not exist in ocean water.

8. The tracheae and cortical bundles are evidently more or less rudimentary and possibly represent useless structures handed down by heredity.

THE REPRODUCTIVE ORGANS

Morphology of the Flower

As a preliminary to the account of the development of the flower and of the reproductive organs, it will perhaps be in the interests of clearness to preface a short description of the mature flower. In this connection I shall also take occasion to discuss briefly some of the more important morphological aspects of the flower.

The flowers of *Ruppia maritima* are small, (3–5 mm. in diameter), consisting of two stamens and generally four pistils, with no perianth, and are borne in a pair at the apex of the peduncle, occurring one above the other, on opposite sides of the rhachis (Pl. IX, fig. 49). The inflorescence is thus spadix-like, a type which is more pronounced in Potamogeton and Zostera.

The mature stamen resembles two thick, rounded, semicircular bands closely appressed to the rhachis (Pl. IX, fig. 49), and meeting each other on opposite sides of it, each band being the half of an anther. In the Bonn Textbook (1908, p. 422), these anther-halves are called "thecae," and because this term is shorter and more specific, it will be used in this paper. A comparison with figure 474 of that textbook (1908, p. 422) demonstrates how a stamen of this sort could easily be evolved by a gradual separation of the thecae. In Ruppia their complete separation at maturity has led them to be interpreted as single stamens with bilocular anthers, for Roze (1894, p. 476) says: "Je n'ai pu y parvenir, car je n'ai jamais trouvé, dans les anthères même jeunes, une adhérence, une soudure quelconque qui le (i. e., cette diminution du nombre des étamines) fît supposer. Et il est bien certain qu'à la maturité des organes, il est impossible de ne pas reconnaître que chaque fleur présente quatre étamines parfaitement libres, ce qui est le point essentiel." Pl. IX, fig. 50, however, gives a correct idea of the morphology of these thecae; for at this young stage the connective shows clearly that the structures on each side of it are merely the two thecae of the same stamen.

At this point, it is interesting to note in Pl. IX, fig. 50 the extension of the connective out beyond the plane of its attachment to the thecae, forming what is described by Irmisch (1851, p. 84) as "ein

kurzer, abgestumpfter, zuweilen etwas ausgehöhlter freier Fortsatz." This develops still further during the growth of the young flower, and sections of it are shown in Pl. IX, fig. 51. Irmisch suggests that this structure corresponds to the pseudoperianth-segment of Potamogeton, which Ascherson (1889) describes as a perianth-like dorsal appendage of the connective. A similar development appears in Posidonia (Ascherson, 1889). That Ascherson agrees with Irmisch's interpretation, is shown by his generic characterization of Ruppia: "Stb. 2, mit sehr kurzen, von den Antherenhälften überragten Anhängseln des Mittelbandes" (1889, p. 207). Eichler (1875, Pt. 1, pp. 89–91) had also supported Irmisch's view.

Čelakovský (1896, pp. 48, 49), on the other hand, believes that these scaly outgrowths from the connective represent reduced floral leaves (Perigonblätter), and deprecates the supposition that they are morphologically portions of the anther connective. Eichler and Ascherson get their strongest argument, of course, from Potamogeton, which shows such a stronger development of this anther-connective structure. Even here, however, Čelakovský (1896, l. c.) sees only floral leaves which have become attached to the connective at its base, mentioning Hegelmaier's (1870) work as one foundation for his opinions.

The development from the connective in Potamogeton resembles strongly a floral leaf, although its connection with the anther-connective is quite pronounced. In the mature flower of Ruppia, after the stamens have fallen away, the same sort of structures may be seen, two in number, at the base of the group of four pistils, and opposite each other. These small structures show a very minute projection, the outgrowth of the connective, as was noted in the young flower (Pl. IX, fig. 50) and below, on opposite sides of it, the scars showing the places where the thecae were formerly attached.

Without going into detail, my own opinion is that the connective outgrowths in Potamogeton represent morphologically perianth segments; that is, I agree with Čelakovský, and if this interpretation is true for Potamogeton, it must be true also for the evidently closely related Ruppia, which, as Čelakovský (1896, p. 49 and 1900, p. 49) emphasizes, is a reduced flower. The reduction is shown not merely in the smaller number of floral whorls, but in this rudimentary condition of the perianth segment.

It will be seen that the appearance of the thecae in the young stage represented by Pl. IX, fig. 50 is much different from that in Pl. IX, fig. 49. As the rhachis elongates, the thecae grow in a

horizontal direction, around the rhachis, closely following its surface, until finally they nearly meet, as in Pl. IX, fig. 49.

The pistils, occurring between the thecae in a group of four, form a diamond-shaped pattern arranged in a transverse position on the rhachis. Each pistil develops, in the mature flower, into a cylindrical structure tipped with a sessile peltate stigma and containing a single ovule.

As regards the number of the pistils, I have never found it to vary; but Ascherson (1889), who divides *Ruppia maritima,* his only species of the genus, into three subspecies, says in his generic characterization, "4 (selten bis 10)". Roze (1894, p. 479), indeed, makes the number of pistils the main specific difference between *R. maritima* and *R. rostellata,* alleging that the former has eight pistils and the latter four. In this vicinity, however, *Ruppia maritima* seems to have always four.

Eichler (1875, p. 89), Irmisch (1851), and other older authorities do not hesitate to allude to the subfloral leaves of Ruppia (the pair at the base of the inflorescence) as the spathe leaves. This homology is not used, however, by more recent authorities. For reasons already adduced, I have applied to them the name of subfloral leaves. As to the spathe, however, it seems quite probable that a rudiment of it is represented in the floral scale leaf. As has been shown (pp. 99–102), its manner of origin, development orientation, etc. all connect it ultimately with the flower, and although its morphological origin is clearly identical with that of a vegetative scale leaf, its relations to the spadix indicate a spathe-like nature. Since the flower of Ruppia represents a much reduced type, we should expect to find such reduced structures here.[1]

Floral Development

With these remarks on the general morphology of the mature flowers, I shall describe briefly the developmental stages of the young flower, from the time when it is first recognizable until about the period when the archesporial cells first appear. From that

[1] I have already indicated (p. 101) that Irmisch overlooked this spathe-like floral scale leaf, and I had been unable to find any reference to it in the literature. At the last moment, however, I find that Griffith (1851 I, pls. 257, 258 and 259; II, pp. 196 and 198) figured and described this structure, considering it a true spathe, and explaining its origin and development essentially as I have done.

point, however, the gross morphological development will be followed during the history of micro- and megasporangia and male and female gametophytes.

Very early the floral rudiment can be distinguished from the vegetative cone by its greater lateral development, giving it a comparative thickness, and because even here the two protuberances, each of which is to develop into a flower, are already apparent (Pl. IX, fig. 52). In Pl. IX, fig. 53 these two floral primordia have become more distinct. Pl. IX, fig. 54 shows a more advanced stage with the floral primordia acquiring the flattened disk form which characterizes them at this period, and the floral scale leaf which, as has been shown, corresponds to the spathe just appearing. In Pl. IX, fig. 55 all of these parts are still more developed, and in Pl. IX, fig. 56 one first sees evidence of a segmentation of the several parts of the flower. At this point each flower is still disk-shaped with the thecae of the young stamens—or their primordia—as four swellings situated diametrically opposite one another—the central part of the disk being elevated and representing the region of the future pistils. The rhachis also first appears well developed here, at least at its base.

Three points of interest will be noted in this early floral development:—

1. The origin of the flowers is lateral, forming a type of inflorescence which is not uncommon, and explained on the hypothesis that the nourishment of the vegetative cone is appropriated by the lateral members (Goebel, 1898, pp. 178, 179).

2. Both flowers in the spadix are of the same age. Their origin in the periblem takes place almost simultaneously, and they remain contemporaneous throughout their entire development. This occurs also in Potamogeton, according to Hegelmaier (1870).

3. The development of the anthers precedes that of the pistils.

Subsequently, the pistils appear as four rounded prominences. These develop by degrees, (but always much behind the staminal development) into the mature, rather cylindrical ovaries surmounted by sessile, peltate stigmas (Pl. X, figs. 58–66).

Microsporangium

The initial cells of the archesporium are first clearly recognizable at such a stage in the floral development as is represented in Pl. XI, fig. 68, where the length of a single young flower in section is

about 0.2 mm. and is about midway between the stages represented in Pl. IX, figs. 55, 56. This stage is signalized externally by the definite appearance of the primordia of pistils and stamens.

Pl. XI, fig. 67 shows the region marked x in fig. 68, being the same section at a higher magnification, and reveals the cells in one of the thecae of the upper stamen. The initial cells, indicated by shading, are distinct from the surrounding tissue by reason of their large size, their large nuclei, their dense cytoplasm, and especially their strong reaction to stain. In these respects, all are essentially alike.

As is apparent, not only the hypodermal layer, but also several of the deeper-lying plerome cells contribute to this group, and since they grade off imperceptibly into the sterile tissue below the theca, it is well nigh impossible to draw a hard and fast line of separation. Thus, it is quite probable that more of the interior cells than I have designated are archesporial.

A point of interest in this connection, and, indeed, an additional proof of the identity of these cells, is their previous history. Up to about the stage represented in Pl. IX, fig. 55, the divisions of the meristematic tissue comprising the flower rudiment follow one another in rapid succession. From that period on, however, there is a slight pause in karyokinesis, with the exception of the divisions in the epidermal region, so that a count of the cells reveals practically the same number in Pl. Xl, fig. 67, as at the end of the meristematic condition. But, in the meantime, a considerable enlargement, cell for cell, has occurred. There is, then, previous to the first unmistakable appearance of the archesporium initials as shown in fig. 67, a brief cessation of cell division, more or less complete, during which occurs a marked increase in their size.

In one of the Potamogetonaceae at least, namely, Zannichellia, more or less uncertainty has always invested the origin of the archesporium. Warming (1873, p. 28), long ago, in his study of this plant, was of the opinion that the sporogenous cells did not arise from a single archesporial layer, but was unable to state just how they did originate. Recently, Campbell (1897, p. 41), in his study of the same plant, says,—"The origin of the sporogenous tissue of the anther is not easy to trace, as the archesporial cells are at first hardly distinguishable, either in form or contents from the adjacent cells. As soon as they are recognizable, there is already a group of them whose relation to each other is not entirely clear."

In his work on *Ruppia rostellata* (1902, pp. 4 and 5) Murbeck, indeed, locates a hypodermal archesporial initial layer, which is quite in line with the vast majority of results so far obtained among the Angiosperms. These hypodermal cells divide into primary parietal and into primary sporogenous cells, which develop in the usual way.

As is evident, Murbeck's report does not correspond with what I have seen in *Ruppia maritima.* But the statements of Warming and Campbell are strong evidence that the state of affairs I have described is quite possible. It is well known that Campbell has found a plerome origin for the archesporial cells in *Naias* (1897, p. 13) and in *Lilaea subulata* (1898, p. 8). A careful study of the history of the archesporial initials in *Ruppia maritima* from the meristematic stage, as outlined above, leaves no room for doubt that we are here dealing with a comparatively large group of cells which originates simultaneously both in plerome and periblem. Very probably, as Warming's and Campbell's studies indicate, Zannichellia develops in a similar way. The archesporial initials of *Lemna minor*, as figured by Caldwell (1899, figure 13), to whose paper I shall have occasion to refer more at length later, closely resemble those of *Ruppia maritima.* On the other hand, Wiegand (1899, p. 344) finds the archesporium in Potamogeton traceable to a single hypodermal cell.

Pl. XI, fig. 69 shows a more advanced stage, the length of the young flower (fig. 70), measured as in the preceding case, being about 0.25 mm. One or two divisions have occurred evidently in all the cells. Although the cells representing the parts of the mature microsporangium are as yet entirely undifferentiated as to their contents, yet the manner of cell-division and the orientation of the walls give evidence of a commencement of a differentiation. First, the majority of the hypodermal cells have divided by a periclinal wall, thus separating off the primary parietal layer. Second, at the left of the top of the figure, there is the first indication, by characteristic periclinal and anticlinal divisions, of the future septum dividing the two sacs of the theca.

In Pl. XI, fig. 71, with a length of flower about 0.3 mm, this wall of separation between the two sacs becomes quite distinct. Its cells have a much less dense content than the archesporial cells, and are thus clearly marked off from them, as well as by the orientation of their walls.

A parallel case of a wall formed in an exactly similar way has recently been found by Caldwell (1899, pp. 47, 48) in *Lemna minor.* Coulter and Chamberlain (1903, pp. 39, 40) in commenting

on this condition in Lemna, say, "To divide a large sporogenous mass by sterile plates for better nutrition is too common to call for special remark." As mentioned by Caldwell and Goebel (1898, p. 770), Isoetes presents a similar condition of formation of sterile plates of tissue from a fairly large archesporial mass.[1]

The archesporial cells, therefore, now appear as two definite, rounded, densely staining masses, composed of sporogenous cells, surrounded by a primary parietal layer, which has undergone a periclinal division in two or three places.

The first periclinal divisions in the primary parietal layer have become more general in the next stage, Pl. XI, fig. 73, which is from a flower about 0.33 mm. in length. The septum between the two sacs is also more conspicuous, and divisions continue in the sporogenous tissue.

At a considerably later period, with the length of the flower about 0.5 mm. (Pl. XI, fig. 74), the parietal layers are still two or occasionally three in number. Indications appear here that the tapetum is forming from the marginal sporogenous tissue. Nuclear divisions continue among the sporogenous cells.

Soon after this stage, however, the sporogenous cells attain their final number, and all division ceases, followed by an enlargement to the mature pollen mother-cells, just as Murbeck (1902) has recorded for *Ruppia rostellata.*

Pl. XI, fig. 75 shows how the tapetal cells, now unmistakable in form and structure, bound the sporogenous cells—which may now be termed the pollen mother-cells—and are undoubtedly derived from them. According to Rosenberg (1901, II), Zostera also forms tapetum from the ends of its long sporogenous cells, and Coulter and Chamberlain (1903, p. 37) have shown that this is not unusual nor unnatural. In this respect, together with the number of chromosomes in the dividing sporogenous cells, which I have found to be 16, and also the three or four parietal layers between the epidermis and tapetum, *R. maritima* corresponds exactly with *R. rostellata*, as described by Murbeck (1902, p. 5). It is interesting to note here that Wiegand (1899, pp. 344 and 345), finds in *Potamogeton foliosus* that the tapetum is "differentiated from the wall rather than from the archesporium."

There remain to be mentioned the dissolution of the tapetal cells (Pl. XI, fig. 76), the development of thickenings in the subepidermal layer, and the final dehiscing of the anther by a longitudinal split.

[1] A like situation has been carefully described by Bower (1897, pp. 41 ff.) for Danaea and other Marattiaceae.

Megasporangium

The usual method of development of the megasporangium corresponds in every particular to that of *Ruppia rostellata*, as described by Murbeck (1902, pp. 10, 11), so that it would be useless to duplicate his careful description here. Stated briefly, the process is as follows: At a stage in the growth of the pistil represented in Pl. X, fig. 62, or when it is about 0.25 mm. in length, a hypodermal cell in the young nucellus, in the region marked x, becomes considerably larger than its neighbors, with a larger nucleus, and more densely staining contents. This then divides by a periclinal wall, forming an outer, primary parietal cell, and an inner, megaspore mother-cell. The primary parietal cell now divides twice successively by anticlinal walls, at right angles to each other, forming a plate of four cells, or, through a third anticlinal division, sometimes six cells.[1] During this time the two integuments successively make their appearance. Meanwhile, the megaspore mother-cell enlarges, and with preparations for the first reduction division the history of the female gametophyte begins.

In Zannichellia, Campbell (1897, pp. 45, 46) finds two parietal layers formed at first, but these later divide into several layers. A much greater development of parietal tissue has been observed by Wiegand (1900, pp. 31, 32) in *Potamogeton foliosus* and by Holferty (1901, p. 341) in *Potamogeton natans*. In the latter case it is definitely stated that sometimes eight layers lie between the embryo sac and the epidermis. In other respects the development of the megasporangium in both of these genera is essentially the same as in Ruppia. In Lemna, according to Caldwell (1899, pp. 56, 57), there are not more than two parietal layers formed, and the other details of the megasporangial development are practically the same as in Ruppia.

Coulter and Chamberlain (1903, p. 65) state that the suppression of the parietal tissue among the monocotyledons "is usually associated also with the greater or less development of this tissue," a point which is illustrated here in the Potamogetonaceae by the condition in Potamogeton. "The strongest argument," to quote these writers further, "that suppression of the parietal tissue of the megasporangium is a strong tendency among Angiosperms, is that this condition is universal among the Sympetalae so far as investigated."

[1] Rarely two layers of parietal cells are formed (Fig. 78).

Before I leave the account of the megasporangium, two cases in which the archesporium was undoubtedly two-celled should be recorded. Murbeck (1902, p. 11 and figure 35) has figured a double megaspore mother-cell, which, however, according to his explanation, is caused by the very oblique orientation of the wall between primary parietal and primary sporogenous cells, making this wall almost perpendicular to the epidermis and hence resulting in two large cells, apparently both potential megaspore mother-cells, and bounded exteriorly by the epidermis.

But my first illustration (Pl. XI, fig. 77) shows a clearly differentiated, single, parietal layer and two large megaspore mother-cells with their common wall very distinct and quite perpendicular to the epidermis. The second example has developed somewhat further (Pl. XI, fig. 78), the two megaspore mother-cells having passed through the first division, a cross wall being formed, which divides each into two essentially equal daughter-cells. Here may also be noted the rather uncommon occurrence of two parietal layers.

On the analogy of the microsporangium of Angiosperms, it would seem most natural that multicellular archesporia should occur also in the megasporangium. Through the investigations of Strasburger (1879), Fischer (1880), and among others, especially Péchoutre (1902), we have come to know that such a multicellular archesporium is quite general in the megasporangia of the Rosaceae; and that it also occurs in many other dicotyledonous groups has been sufficiently proven.

On the other hand, the reports of an archesporium of more than one cell in the megasporangium of monocotyledons are meagre, and, as reviewed by Coulter and Chamberlain, may be embraced in two cases, *Ornithogalum pyrenaicum* (Guignard, 1882), and *Lilium candidum* (Bernard, 1900). In these instances the archesporium is presumably always more than one-celled. There are, however, many cases, such as some of the Ranunculaceae, when the archesporial cells vary from one to many (Mottier, 1895, and Coulter, 1898). To such as these last the condition in *Ruppia maritima* is similar.

Female Gametophyte

As it is now regarded, the history of the female gametophyte commences with the preparations for the first division in the megaspore mother-cell. As regards this preparatory stage, I find that *Ruppia maritima* does not deviate essentially from *R. rostellata*,

and I have, therefore, no occasion to alter or add to Murbeck's excellent description.

In brief, the changes are very similar to those which lead up to the first division in the pollen mother-cells. The megaspore mother-cell and its nucleus enlarge, while the latter goes through the synapsis and succeeding stages, the staining reactions being essentially the same and even the fine kinoplasmic fibers appearing in the cytoplasm the same as in the corresponding stages in the pollen mother-cell.

In the spindle formed for the first reduction division, eight chromosomes appear (Pl. XII, fig. 80), as Murbeck also announces in *Ruppia rostellata.* Although the chromosomes are here much thicker than in the sporophytic karyokinesis, they are nevertheless still so small that any definite declaration concerning their shapes and method of splitting is well nigh impossible. Still, as Murbeck has noted, the ring and Y-shaped forms characteristic of the heterotypic division are occasionally apparent.

After the nucleus of the megaspore mother-cell has divided, we find a wall laid down separating the two daughter-cells (cf. Murbeck, 1902, fig. 45). In this connection, reference might be made to the case already noted under the megasporangium (p. 136), where a double megaspore mother-cell was found, producing in each case two such daughter-cells (Pl. XI, fig. 78).

The second division follows closely on the first, with a very slight pause, similarly as in the pollen mother-cells. The two walls resulting from these divisions are, however, laid down at quite different planes with respect to each other, that is, the wall dividing the two inner cells is periclinal, while that separating the two outer is anticlinal. Thus the two outer cells are both in contact with the third cell, and are separated by it from the innermost cell. The plane of the anticlinal wall is, however, obliquely situated with regard to the plane of a horizontal or vertical median section of the megasporangium; in other words, it is oblique to the plane of the paper on which such a section is represented, so that an oblique position of the two upper cells with respect to this plane results.

This arrangement is shown by Murbeck (1902, pp. 13, 14, fig. 51). But often, due partly to the manner of cutting the section and partly to the orientation of the outer anticlinal wall, the position and even the number of cells is not so apparent, since one of the two upper cells then lies more or less completely over the other. Such a case is represented in Pl. XI, fig. 79, which a hasty

glance might have interpreted as three megaspores, the upper two becoming resorbed. But careful focussing discloses another outer cell at a somewhat lower plane. Murbeck (1902) figures a similar case in *Ruppia rostellata.*

This departure from the usual method of division of the megaspore mother-cell, in which, in general, the resulting cells are formed in a straight row, is fully commented upon by Murbeck (1902, p. 13), who states that it has been found also in *Allionia nyctaginea, Helleborus foetidus* and *Ceratophyllum demersum*; and to his work I refer for a fuller account of the whole matter and for literature bearing upon the subject. A concise morphological consideration of such a location of the potential megaspores is also set forth by Coulter and Chamberlain (1903), who although they do not mention the case of *Ruppia rostellata*, note a similar arrangement of the outer two cells as occurring in Butomus (Ward, 1880), Jeffersonia (Andrews, 1895), and Potamogeton (Holferty, 1901).

Moreover, that this position of megaspores is not an invariable rule in *Ruppia maritima*, is shown by such a case as is illustrated by Pl. XII, fig. 81, where the four cells appear in a row, the two outer ones already much disorganized.

Before proceeding further, the condition shown in Pl. XII, fig. 82 should be noted, where the nucleus of the upper of the two daughter-cells has divided, but no wall has been formed, and the whole cell, along with its neighbor below, is undergoing resorption. Such a happening seems natural when one reflects that the division in the lower daughter-cell in general precedes that in the upper cell, producing a tendency by the earlier development of the former, to reduce activity in the upper daughter-cell. It will be seen later that this omission of the wall in the upper daughter-cell is the ordinary occurrence in *Potamogeton foliosus.*

In all cases the lowest of these four cells becomes the functional megaspore, the upper three cells becoming resorbed, as in *Ruppia rostellata* (Murbeck, 1902, pp. 14, 15).

In *Potamogeton natans*, Holferty (1901) describes cases of four megaspores with the same arrangement as in Ruppia, the innermost functioning.

In *Potamogeton foliosus*, described by Wiegand (1900), the condition is quite different and yet exhibits points of similarity. The first reduction division produces two daughter-cells, separated by a wall. The second division then takes place in each of these cells, and the resulting nuclei occupy practically the same positions as they do in Ruppia. No walls are formed after this division,

however. If they were, it is evident that a tetrad similar to that in Ruppia would have resulted. The upper daughter-cell with its two nuclei now becomes disorganized, and the lower cell becomes the embryo-sac, its nuclei producing directly the embryo-sac nuclei.

Zostera marina forms three megaspores, according to Rosenberg (1901, I, p. 9), the lowest functioning. The uppermost, however, in his Figure II looks much like Figure 51 of Murbeck (1902), and like many of my own preparations, gives indications of two cells obliquely arranged.

In Zannichellia the state of affairs is surprisingly different. According to Campbell (1897, pp. 45, 46), a row of three cells is formed, of which the uppermost becomes the functioning megaspore. Since this is so strikingly diverse from what takes place in Ruppia, Zostera and Potamogeton, it would seem as if it needed confirmation.

The functional megaspore now proceeds to the formation of the embryo-sac by a series of stages which are quite in line with those which have been found to be so remarkably constant among the Angiosperms. Pl. XII, fig. 82 shows the megaspore nucleus in process of division, while Fig. 83 discloses the resulting two nuclei, one at each end. Fig. 84 shows the four nuclei coming from these two. Fig. 85 represents a mature embryo-sac with synergidae and egg of characteristic form and structure. The antipodal cells are always three in number, their nuclei being surrounded by a definite layer of cytoplasm and apparently by a thin, membranous wall. Often they appear rounded in form (Pl. XII, fig. 85) and again angular (Fig. 86), in the latter case showing clearly their relations to each other. They resemble strongly those figured by Murbeck (1902, fig. 53) in *Ruppia rostellata* and by Campbell (1897, fig. 109) in *Zannichellia palustris*, and like them are situated in a small pouch at the base of the embryo-sac.

A peculiarity of these antipodals is the conspicuous blue color of their nuclei with the triple stain, showing an unusual tint of the blue, and possibly indicating degeneration. Thus they are strongly contrasted with adjacent nucellar nuclei and may be readily distinguished. They were not observed to divide, however, as in the case of certain recently investigated monocotyledons. Apparently their life is short, for they disappear in stages slightly older than Pl. XII, fig. 85.

Male Gametophyte

Since my studies of the male gametophyte of *Ruppia maritima* agree closely with those of Murbeck (1902), it would be useless here

to go into a lengthy description. For the sake of completeness, however, I will review the more important points, noting a few minor differences from Murbeck's results, and adding a few observations of my own.

We may regard the history of the male gametophyte as beginning with the appearance of the synapsis stage in the pollen mother-cells, which precedes the first reduction division and signalizes the special preparations for that process. Seven different flowers chanced to be fixed during this stage, and the appearance of the pollen mother-cells in all was typical (Pl. XII, fig. 87). The nuclei are very large, but no knoblike processes are appended to them, such as Wiegand (1899) figures for *Potamogeton foliosus.* Although some such appearance was occasionally found, it was not sufficiently general to be called typical of this stage.

In the first reduction division I succeeded in finding several cases of multipolar spindles, as Murbeck (1902, p. 7) has also reported. The two reduction divisions follow one another in rapid succession, forming a tetrad, whose members are oriented to each other after the manner of the four quadrants of a somewhat elongated sphere (see Murbeck, fig. 16). A similar arrangement is figured by Bornet (1864) in Cymodocea, and is not uncommon in the monocotyledons in general. During the two reduction divisions I was able in several cases to count eight chromosomes, which is, therefore, the reduction number, as Murbeck (1902) also found in *Ruppia rostellata.*

In the study of the development of the pollen-grain, as in other structures, I found it of advantage to use a certain definite method of external measurement as an index to the stage of internal development. Thus, in the case of the pollen-grain, I chose the length of the grain, which, from its first formation in the tetrad to the mature condition, increases from about 175 μ to about 550 μ. Although these dimensions are subject to some variation, even in the same pollen-sac, yet they are fairly constant for the same period of growth.

At the time of the formation of the tetrads the nucleus is in an approximately central position. Very soon after, or while the grain is still not much more than 175 μ in length, the nucleus shows a position nearer to one end of the grain (Pl. XII, fig. 88), and a central zone of small starch grains has appeared. Almost immediately thereafter one finds the nucleus at the end of the grain, the starch grains having become considerably larger and uniformly distributed (Pl. XII, fig. 89). A nuclear division now ensues (Fig. 90), and as a result, the small lenticular cell at the end of the grain, the generative cell, is formed (Fig. 92).

As to the number of chromosomes distributed to the daughter-nuclei in this division, it is impossible to state it exactly, after a careful study. Murbeck, however, succeeded in finding a very clear case where eight appeared in the nuclear plate, and judging from the count in the two preceding mitoses, and also from general appearances in the division, it appeared to me as if eight was the most probable number in *Ruppia maritima.* The chromosomes in this division, as in the much later one when two male cells are formed (p. 142), are extremely small—much smaller than in the first and second divisions in the pollen mother-cell—so that even with the highest powers of the microscope they are very difficult to identify.

A few words should be added regarding the generative cell at this period. As Murbeck has noted, its nucleus is smaller than the tube-nucleus, but, judging from the staining reactions of the two, it contains a comparatively larger amount of chromatin. Moreover, a definite aggregation of cytoplasm surrounds the generative nucleus. As Murbeck has announced in *Ruppia rostellata,* so here no membrane separates this cell from the rest of the microspore, and it is evident that one sees here a naked cell, such as occurs in the case of the egg or synergidae of the embryo-sac. On the other hand, Wiegand (1899, pp. 352, 353, figs. 41, 42) finds the generative cell in Potamogeton—which, by the way, is not formed until the "spores reach their full size"—enclosed in a definite membrane. A distinct wall is also found in Typha by Schaffner (1897. I.) and in Naias and Sparganium by Campbell (1897, 1899). Rosenberg (1901. I.) in Zostera mentions only a very indistinct wall at a later stage, when the two male cells are formed, separating them from the surrounding pollen-plasm.

In most cases, though by no means always, a narrow space separates this cell from the rest of the microspore, which a study of a large number of sections shows is undoubtedly due to a contraction. (Pl. XII, fig. 92).

The microspore now enters upon a long period of growth, during which it increases in length from the 175–225 μ of the above described stages to the 500–550 μ of the mature condition. During this period it gradually assumes its curious bow-shaped form, with the characteristic dumbbell-like expansions at the ends, and also a considerable dilatation centrally at the convex side of the bow (Pl. XII, fig. 95).

A pollen-grain so remarkable in shape is not unique among the Potamogetonaceae; for the pollen-grain of Cymodocea is also unusual, being a long filamentous grain measuring, according to Bornet

(1864), ten by about two thousand μ, while the microspores of Zostera (Rosenberg 1901, II) are three by about two thousand μ when mature. Moreover, in Phyllospadix, grouped by Ascherson (1889) with Zostera in the subfamily Zostereae of the Potamogetonaceae, Dudley (1893) has found the pollen grains to measure about four or five by one thousand μ. Dudley (1893, p. 412) states that "They are slightly flattened at the extremity and some are enlarged toward the middle."

During this long period of development to the mature form, several noteworthy internal changes occur. The tube-nucleus (Pl. XII, figs. 92, 93 *tn*) gradually undergoes degeneration, until in the mature grain it often appears fragmentary or angular. The starch grains, so prominent in the early stages, become for the most part smaller and fewer, and one seems warranted in concluding that a part of their substance has been utilized in the formation of the grain.

It is not until the mature condition, or when the pollen is about ready to be discharged, that the generative cell divides. When this is to take place, the latter assumes a position in which its long axis is more or less parallel with the long axis of the microspore. The two resulting male cells remain united as in *Potamogeton foliosus* (Wiegand, 1899), each surrounded by a considerable layer of cytoplasm (Pl. XII, fig. 94).

Moreover, even at this stage, no wall separates the male cells from the cytoplasm of the pollen-grain, but there is a fine cell-plate formed between the two cells. As a slight variation from Murbeck's figure, I find that for the most part in *Ruppia maritima* a moderate constriction occurs between the two male cells, in the region of the cell-plate.

One feature which has not been thoroughly worked out in the pollen-grain of Ruppia and indeed has been much neglected in the study of the male gametophyte in general, is the origin and growth of the microspore wall.

Murbeck (1902) has described the peculiar thickenings of the mature wall, the latter consisting of a single thin layer.

Since I was fortunate enough to have a large number of sections of all stages of the growth of the pollen-grain, the development of the wall from the pollen mother-cell stage to the mature microspore was comparatively easy to trace.

The wall of the pollen mother-cell, after it has separated from its neighbors, is very thin. After formation of the tetrads, this wall thickens and becomes the free or outer wall of the tetrads, while the interior walls of the tetrad are laid down immediately after the two reduction divisions, Pl. XII, fig. 88. These tetrad cells do

not separate: the protoplasts forming the future pollen grains may be said to simply occupy the four quadrant-like compartments in the spherical structure comprising the tetrad. The walls at this stage are of noteworthy appearance by reason of their considerable thickness—being thicker than the wall of the pollen-grain at any future time—and also from their transparency, refracting the light in such a way that they appear gelatinous.

The tetrad walls appear now to expand, leaving the pollen protoplasts naked within them. Such a condition is shown in Pl. XII, fig. 97. Finally the walls entirely dissolve.

Judging from Murbeck's account, these conditions escaped his notice, for he speaks of the *membrane of the tetrads* as showing "noch keine Spur von Oberflächenstruktur" (1902, p. 8).

The process is, however, essentially the same as that described by Strasburger (1882, pp. 87 ff.; 1889, pp. 36 ff.) for the pollen-grain of *Malva crispa* and other plants. Only one marked difference occurs, namely, that in *Malva crispa*, &c. the old pollen mother-cell wall is apparently cast off and does not take part in the wall formation of the tetrads.

From now on a wall develops around the young pollen-grain, but, as in the cases of Naias and Zannichellia, remains a single thin membrane (Pl. XII, fig. 94).

Very early (Pl. XII, fig. 97) the local thickenings begin to be formed on the outer surface of the wall. These in this early stage are difficult to see clearly on account of their transparence. They seemed, however, to be the result of depositions on the wall and not do develop from radial bands in its interior. Ultimately these thickenings appear in the shape of low ridges arranged to form irregular polygons, at whose intersection are short spines, with a slight knob at the end (Pl. XII, fig. 96, *a* and *b*). At the ends of the grain and at its expanded center, these spines become shorter, or are absent altogether (Pl. XII, fig. 94). It is probable that at these localities the pollen tube commences its formation.

Pollination

Ruppia is one of the few of the higher plants to which, in respect of the process of pollination, the term hydrophilous may be applied. In other words, water is the transporting agent for the pollen, instead of the commoner methods by insects or the wind.

According to my own observations, which agree in the main with those of Roze (1894), the process of pollination takes place about as follows. Soon after the extension of the peduncle above the surface of the water, the anther sacs split open by a longitudinal cleft, and the pollen, shed in large yellowish masses, may be seen floating on the surface of the water.

Immediately subsequent to the shedding of the pollen, the rhachis, which up to this time has been erect, commences to incline toward the surface of the water. It becomes more and more horizontal until eventually, after two or three hours, it comes to lie on the surface of the water.

In this position, the stigmas are of course so situated that the floating pollen grains, with which, in the height of the flowering season, the water is fairly well covered, have easy access to them. The final step occurs when the currents of water, always moving in one direction or another in a tidal ditch—or sometimes set in motion by gusts of wind—bring the pollen grains into contact with the stigmas.

Wylie (1904), has described a similar mode of pollination in Elodea. He attributes the floating of the pollen-grains to the air imprisoned between the spines of the pollen-grain and the surface of the water, this being sufficient to keep the grain afloat. Pollination on the surface of the water also takes place in Vallisneria, as is well known. In Zostera, however (Strasburger, 1908, p. 258), pollination is performed below the surface of the water.

Fertilization

No investigator has yet been able to demonstrate the process of fertilization in Ruppia. Murbeck (1902, p. 15) has, indeed, found the pollen tubes in the ovary; but has been unable to distinguish either of the sperm-nuclei in the embryo-sac. For various reasons, he concludes that the act of fertilization takes place very rapidly. If this is true, it may account for the fact that in my own preparations I also have been unable to find any unmistakable evidence of the sperm-nuclei.

As is shown in Pl. X, figs. 62–66, a definite stylar canal exists from the stigma to the cavity of the ovary, but Murbeck (1902, l. c.) claims that the pollen tubes, however, penetrate through the cellular structure of the style to the cavity of the ovary.

Endosperm

The endosperm nucleus is large, and located near the antipodal end of the embryo-sac, or sometimes near the center. Just what nuclei enter into its formation was not ascertained, nor could I determine whether or not in the matter of commencing division it has a slight advantage over the fertilized egg, as Murbeck (1902) declares is the case in *Ruppia rostellata.*

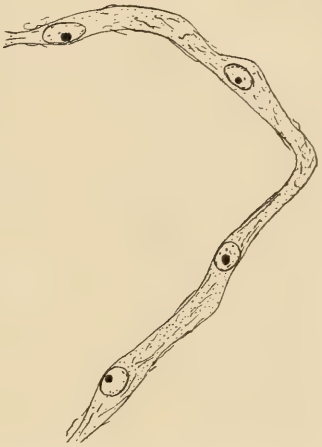


Figure 27.—Portion of endosperm which lines embryo-sac, this particular example being taken from the embryo-sac which contains the embryo shown in Pl. XIII, fig. 106. × 575.

The endosperm in its most fully developed stage (Text-fig. 27), is never more than a thin layer lining the embryo-sac and containing free nuclei. In the mature seed, traces of it may still be seen as a thin protoplasmic lining, with the nuclei now much reduced in size. Thus it is clear that the endosperm is here only temporary. The function of more lasting nourishing tissue is assumed by the enlarged hypocotyl. A similar development of endosperm appears in other Potamogetonaceae (Coulter and Chamberlain, 1903, p. 171).

EMBRYO

The fertilized egg divides transversely, producing al arge lower cell and small upper cell. As in Naias (Campbell, 1897, p. 26), Zannichellia (Campbell, l. c., pp. 27, 28), Zostera (Rosenberg, 1901, I; Hofmeister, 1852), and Potamogeton (Wiegand, 1900), the former divides no further, but subsequently increases vastly in size, developing large vacuoles, and becomes the suspensor, which is thus in this case restricted to a single large, basal cell.

I was unable to discover any stages between the two-celled proembryo and the twelve-celled stage—the latter represented in Pl. XIII, fig. 100. Murbeck, however, figures a three-celled stage in *Ruppia rostellata,* which I reproduce (Pl. XIII, fig. 98), showing two small cells, which may be called the "embryo-cells," arisen from the transverse division of the small upper cell; and also the basal large cell, namely, the suspensor-cell. Wille (1883) figures and also describes a similar stage in his work on the embryo of *Ruppia rostellata.*

Wille has carefully followed the development of the proembryo in these early stages, and his observations and figures accord well with my slightly older embryos. His report of the succeeding divisions is briefly as follows: The lower of the two embryo-cells divides longitudinally, followed by a similar division in the same plane in the upper cell, making four cells in all; next, by longitudinal divisions in both segments, in a plane at right angles to the last, an eight-celled structure is formed. The embryo now consists, therefore, of two four-celled segments lying one over the other, and borne on a single large suspensor-cell (Pl. XIII, fig. 99.)

It should be borne in mind that this suspensor cell is the basal segment resulting from the first division of the fertilized egg, and never again divides. In this connection it may be well to follow out the subsequent history of this peculiar suspensor before going into an account of the embryo proper.

After the first unequal division in the fertilized egg-cell, the suspensor-cell becomes rapidly larger, and at the time when the two four-celled segments appear, as described above, it is much larger than these combined (Pl. XIII, fig. 99). At the period shown in Fig. 100, when the embryo contains twelve cells, the suspensor-

cell nucleus, with the majority of the cytoplasm, occupies a position at the base of the cell, the upper part containing one or more large vacuoles. This appearance, although not invariable (cf. fig. 101), seems a quite general one in the disposition of the cell-contents at all stages except the very earliest. The same has been noted in Zostera (Rosenberg, 1901, I, pp. 11, 12) and Potamogeton (Wiegand, 1900, p. 37).

Although the suspensor-cell is now (Pl. XIII, fig. 100) enormous in size, this is in fact only a stage in its enlargement. Fig. 101 testifies to what proportions it eventually attains. At the same time its nucleus attains a large size. In somewhat later stages the suspensor-cell commences a gradual disintegration, until, at a period of embryo development, such as in fig. 106, the outlines of the cell can be no longer distinguished, although its nucleus is still apparent in a condition of disorganization.

During its development, the suspensor-cell is in contact with the micropylar end of the embryo-sac for some time, but may eventually become free, as Wiegand (1900, pp. 37, 38) has also noted in Potamogeton.

In connection with this remarkable growth, the statements of Rosenberg (1901, I, p. 12), who describes a similar suspensor in Zostera, may be quoted. In writing of the nucleus of this cell he says: "Der Kern des Embryoträgers .... macht eher den Eindruck, als ob in demselben eine rege Stoffbildung vor sich ginge; etwa eine Aufnahme von Stoffen, die in dem Kern weiter umgebildet werden, um später in das Embryo zu gelangen." It might be added that not only the nucleus, but also the whole cell, judging from its appearance and time and manner of development, has obviously the function of reception and preparation of nourishment for the embryo. It is significant also to note that at the time of the degeneration of this large suspensor-cell, the endosperm nuclei are relatively abundant.

Although a similar large basal cell occurs in Naias (Campbell, 1897, p. 26), Zannichellia (Campbell, 1897, pp. 27, 48), Zostera (Rosenberg, 1901, I, pp. 11, 12) and Potamogeton (Wiegand, 1900, p. 37), only in Zostera does it represent the entire suspensor as in Ruppia. In the remaining genera other small secondary suspensor-cells are formed above the large basal cell.

It will be seen that the three-celled stage of the proembryo (Pl. XIII, fig. 98) is essentially similar to that of Sagittaria (Schaffner. 1897, II, p. 262 and Pl. XXIV figures 46, 47) and Alisma (Schaffner, 1896, pp. 129, 130), which has been regarded as typical of the

monocotyledonous embryo (Coulter and Chamberlain, 1903, pp. 188, 190 ff.).

Instead of the increase of this row of cells from three to four, or, in other words, to a row of three embryo-cells, as is the case in the above-mentioned genera, Wille, as already stated, finds that two plates of four cells each are formed from the two embryo-cells. These two resulting four-celled segments are, nevertheless, still the representatives of the two small embryo-cells, which are formed first, in Ruppia as well as in Sagittaria and Alisma.

That this condition is the usual one in Ruppia is shown not only by Wille's (1883) observations, which may be correlated so well with my own, but also by the figures and description of Hofmeister (1852, p. 143 and figures 41–46, and 1861, figures 1–7, pl. II)[1].

My twelve-celled embryo (Pl. XIII, fig. 100), composed of three four-celled plates, has obviously arisen by a transverse wall through one of these four-celled segments—which one, it is not possible to state. In the typical embryo of Sagittaria, indeed, it is the lower of the two segments that undergoes a transverse division (Schaffner, 1897. II, p. 262 and Pl. XXIV, figures 46, 48, 49), and this may be the case here.

What has occurred then is simply the formation of three segments, one above the other, comparable to the three upper cells in Sagittaria (Schaffner, 1897, II, Pl. XXIV, figures 48, 49), with the difference that in Ruppia longitudinal divisions precede the transverse ones.

A comparison of this stage with those embryos of related genera which have been worked out, brings to light the following points. The embryos of Zannichellia (Campbell, 1897, p. 48 and cf. fig. 63 Pl. III; Hofmeister, 1861, Pl. I, fig. 18) and Potamogeton (Wiegand, 1900, pp. 37, 38, and Pl. VII, figures 25, &c.) are essentially like that of the typical Sagittaria, consisting of a row of three cells above the suspensor-cell, the terminal one being the first to undergo longitudinal divisions.

As to the embryo of Zostera, it was investigated at a very early period by Hofmeister (1852), and quite recently by Rosenberg (1901, I). Their results are not complete in the early stages, but enough has been shown to indicate that Zostera is more like Ruppia in the early development of its embryo than any of the Potamogetonaceae so far investigated. Hofmeister (1852, p. 139) states that

[1] Practically the same figures are presented in each of these articles: in the former, the species is given as *rostellata*, in the latter, as *maritima*.

a four-celled embryo is formed from the first embryo-cell by two longitudinal divisions occurring at right angles to each other, and these quadrant-like cells are next each divided by a transverse wall. So that, although the divisions here occur in different sequence, the two four-celled segments nevertheless result.

Although these first stages were not followed out by Rosenberg, he presents a figure (1901, I, Pl. I, fig. 20, and P. 12) of an eight-celled embryo similar to that of Wille's (Pl. XIII, fig. 99). It is perhaps possible that later investigation will show that the first wall in Zostera is transverse instead of longitudinal, as Hofmeister has described it.

The task of tracing out the lines of demarcation of the primary segments during the later stages, after the manner of recent embryological investigations, is very difficult, probably from two principal causes. First, the remarkable number of early longitudinal divisions which have already been indicated to a certain extent obscure the segment limits. Second, the form of the mature embryo differs so widely from that of a typical monocotyledon that even in the early developmental stages this influence makes itself felt, and renders comparison with type forms rather unsatisfactory. Wille, indeed (1883, pp. 2, 3), describes his eight-celled stage as forming a sixteen celled structure by transverse divisions in all of the eight cells. But of the subsequent divisions he says (l. c., p. 3), "Herefter gaa Delingerne uregelmæssigt, saa man ikke længere med Bestemthed kan følge de enkelte Cellers Delinger."

Of stages older than the eight-celled embryo of Wille and Hofmeister, I was fortunate in having a fairly large number, and in the following description I shall attempt to show to what extent the segment boundaries may be traced during the embryo development, and how they may be correlated to such a type as Sagittaria.

I have already suggested that such an embryo as is represented in Pl. XIII, fig. 100, composed of twelve cells, or three four-celled segments, arises from Wille's younger form by a transverse wall through one of the segments, and that this is parallel to the case in Sagittaria, where a three-celled row arises by a transverse division in the lower embryo-cell.

Fig. 101 is a slightly older embryo, in which the divisions are somewhat irregular, but still admit of an interpretation which reveals the outlines of the cells and segments in the preceding stage. It is evident that a transverse division has occurred in the terminal segment.

In fig. 102 appears evidently the beginning of the formation of the dermatogen, at least in the terminal segment at the left. Fig. 103 shows the segment lines more irregular, the dermatogen has became more pronounced, and in fig. 104 shows a distinct differentiation. A point of interest at this stage is the considerable increase in size of all the cells, which are, however, only slightly greater in number than in fig. 103. The embryo here measures about 0.075 mm. in diameter, as against the 0.05 mm. of the preceding one.

Up to this point the embryo has exhibited a globular form, but in fig. 105, where it measures about 0.085 mm. it has commenced to elongate. It is at this period that the divisions are initiated in the terminal segment, appearing here at the left, which signalize the approach of cotyledonary development.

It has been shown by Schaffner (1897, II, pp. 263–265) in Sagittaria that of the proembryo of three cells, the uppermost develops the cotyledon, the middle divides transversely, and of the two resulting segments the upper develops the stem apex and the lower the hypocotyl, root, and secondary suspensor. The lowest cell of the three-celled proembryo remains undivided, forming the basal suspensor-cell.

Obviously the primary segments in Ruppia do not all have destinies similar to those of Sagittaria. For, to begin with, no secondary suspensor is here found, and only a minute rudimentary root, as will be shown later. Again, it seems quite probable, although for the reasons stated above no conclusions can be certainly drawn, that the terminal segment produces the stem-apex as well as the cotyledon. Campbell (1897, p. 49) finds such a condition in Zannichellia, and the appearances shown in fig. 106 point to such a situation here. Solms-Laubach (1878), as noted by Campbell, has also reported a terminal origin of the stem-apex in some of the Commelinaceae and Dioscoreaceae. This leaves the second segment (which, as has already been indicated, probably divides transversely to form the second and third segments, as in Sagittaria) for the development of the hypocotyl, extraordinarily large in Ruppia, and the small rudimentary root adjacent to the suspensor-cell.

Pl. XIII, fig. 105, however, represents the oldest embryo in which the primary segments can be determined with accuracy. In the next figure (fig. 106), it is quite impossible to make out definitely the line separating the terminal segment from the rest of the embryo, to say nothing of any other segment-lines. Nevertheless, in this embryo, cell divisions are active in the terminal region

and one can easily see a small prominence (fig. 106, *cot*), accompanied interiorly by a number of cell-divisions, which is obviously the beginning of the cotyledon. Moreover, at its right is another markedly meristematic region, the future stem apex or epicotyl (fig. 106, *st*).

Wille's description of the subsequent development up to the mature embryo agrees essentially with my slides, so that I confirm his observations in the main, adding a few details. For the sake of clearness, each member will be described separately.

The Cotyledon. Originating as described above, the cotyledon elongates and the epicotyl develops at its base. In the course of its growth, the cotyledon develops basal sheaths similar to those characteristic of the leaves of a mature plant, which then surround the epicotyl. Concerning this condition Wille (1883, pp. 3, 4) says, "Hos den modne Frugt er Plumulaen ganske omgiven af Cotyledonet (Tavl. I, fig. 25), kun en trang Spalte fører ind til Hulen," but figures an embryo with a large open hollow at the base of the cotyledon, where the epicotyl may be seen. As a matter of fact, in *Ruppia maritima* at least, the cotyledonary sheaths overlap one another for almost the whole of their length, essentially as do the sheaths of the foliage leaves (Pl. XV, fig. 118). Only at the upper end of these sheaths is there a small cleft remaining (Fig. 118, *x*) which may be the "trang Spalte" mentioned by Wille. Thus the sheaths enclose the epicotyl so that it is quite shut off from view. In Pl. XIV, fig. 112, and Pl. XV, fig. 116 these sheaths appear in section in not quite mature embryos, and figures 117 and 118 show them in a cotyledon dissected from a mature embryo. It is interesting to note that the axillary scales may be seen within the sheaths, at their base, as in the mature plant.

Wille (1883, Pl. I, fig. 25) figures the cotyledon as elevated a considerable distance above the hypocotyl, although still extending more or less horizontally, and one might conclude that possibly herein is a specific difference between *Ruppia rostellata* and *R. maritima*, were it not for the fact that Irmisch (1858, fig. 37, pl. I) figures the cotyledon closely appressed to the hypocotyl as I find it in *R. maritima* (Pl. XV, fig. 119). In Text-fig. 28, p. 152, this horizontal position has been slightly disturbed through manipulation.

The Epicotyl. Pl. XIV, fig. 112 shows the epicotyl in a nearly mature embryo. It consists always of a second leaf and the growing point, the latter not appearing as prominently here as in other sections. Wille (1883, p. 3, figs. 25 and 26) is in doubt whether this smaller pro-

tuberance is really the growing point or the third leaf, but a comparison with the growing point of the mature stem (Pl. I, fig. 1; Text-fig. 2, p. 75) conclusively proves its nature.

The Hypocotyl. The great bulk of the embryo is taken up by the hypocotyl (Pl. XV, fig. 119, Text-fig. 28), which is nothing but a mass of storage tissue, its cells being gorged with large starch grains. Even in such a young stage as in Pl. XIII, fig. 105, the cells in this region are distinctly larger than in the remainder of the embryo. They continue their enlargement and acquire an ever richer content of starch as development proceeds (cf. Pl. XIII, figs. 105, 106; Pl. XIV, figs. 110–112, 114; Pl. XV, fig. 115).

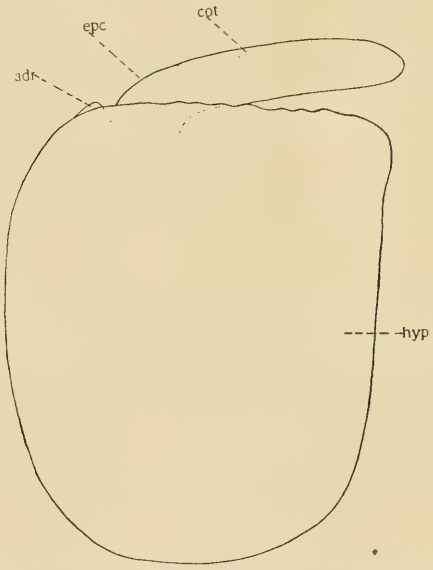


Figure 28.—Mature embryo dissected from ripe seed, the cotyledon slightly elevated during manipulation. *cot*, cotyledon; *epc*, region of epicotyl; *adr*, adventitious root; *hyp*, hypocotyl. × 35.

The Primary Root. At a fairly early period (Pl. XIII, fig. 106; Pl. XIV, fig. 110) a certain group of cells becomes differentiated at the base of the embryo, by acquiring denser contents and lacking the starch grains of the storage cells above them. Each of these cells later develops (at least those on the periphery of the embryo) into unicellular papilla-like projections, essentially as figured and described by Wille (1883, p. 4 and Pl. I, fig. 19) and Murbeck (1902, pp. 17, 18 and figs. 60 b, 61 b). Like Murbeck, I find also often more than a single layer, but whether arising from periclinal divisions in the

dermatogen, as he asserts, I was not able to determine. The whole group is supposed to represent the vestiges of the primary root (Murbeck, 1902, p. 18; Wille, 1883, p. 4), which develops only to this rudimentary degree, and never functions.

The First Adventitious Root. At about the period when the cotyledon and epicotyl have become quite distinct in outline, the formation of an adventitious root occurs near the base of the epicotyl. This grows rapidly, forming a noticeable protuberance (Pl. XIV, figs. 112, 113), and in the mature embryo (Text-fig. 28) may be seen pointing almost directly upward, or nearly at right angles to the position of the cotyledon.

The distribution of the meristematic regions at the tip of this adventitious root is not as clearly marked as in the roots of the mature plant. It will be recalled that the roots of the mature plant, as in Zannichellia, contain at their tip four distinct meristematic regions, representing the initial areas of calyptrogen, dermatogen, periblem and plerome.

In the young adventitious root of the embryo an interesting point is the division of the epidermis of the hypocotyl, immediately over the young developing root, by periclinal walls, apparently to form root cap. These divisions continue, and anticlinal as well as periclinal occur. This is a very different condition from that in the roots of the mature plant.

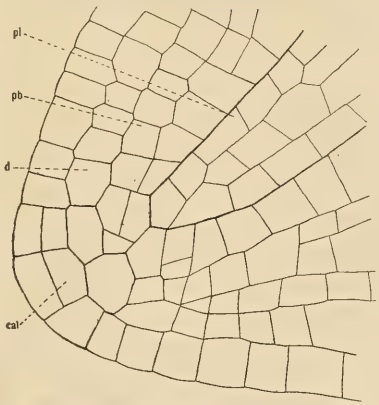


Figure 29.—Longitudinal section through apex of adventitious root of nearly mature embryo; showing *pl*, plerome, *d*, dermatogen, and periclinal divisions initiating development of calyptrogen, *cal*. × 530.

Whether the dermatogen and periblem are each also here represented by a single layer at the apex of the growing-point would be impossible to assert definitely, on account of the irregularity of the cells, but such seems to be often the case (Text-fig. 29). However, some embryos show only one layer for both dermatogen and plerome, as Campbell finds most usual in the primary root of Zannichellia (Campbell, 1897, p. 51). The plerome is pretty clearly marked (Text-fig. 29), but also does not have as definite a point of origin as in the roots of the mature plant.

The mature embryos of *Ruppia maritima* measure 1.5–2 mm. in length, by a little more than 1 mm. in width. Although I find no measurements recorded of the embryos of *R. rostellata*, Irmisch's figure (1858, fig. 37, Taf. I) is somewhat longer in proportion to its width.

Murbeck (1902, p. 18 and Pl. III, figs. 62, 64, and 65) has called attention to the resemblance of this curious embryo of Ruppia to those of the related genera, Zannichellia, Halophila and Zostera. The embryo of Phyllospadix is similar, but characterized by a peculiar lobing of the hypocotyl around the base of the cotyledon (Dudley 1893, p. 413 and Pl. II, fig. H).

To the well known controversy regarding the real nature of the adventitious root and of the primary root, I will briefly allude and record my own views here.

In writing of the Potamogetonaceae, Ascherson (1889, p. 200) says, "Meist entwickelt sich eine kräftige Hauptwurzel an dem unteren Ende des Embryos; nur bei Ruppia befindet sich dieselbe seitlich neben der Plumula."

Thus Ascherson, whose view has been adopted by Goebel (1898, pp. 464–466), rejects the conclusions of Wille, who found the peculiar cell-group developed in *R. rostellata*, which I have also reported for *R. maritima*, at the base of the hypocotyl and immediately over the large suspensor-cell. This basal region is, as Wille says, the place for the primary root of the embryo. Wille, therefore, considers this the rudiment of the primary root, and the structure near the base of the plumule, which Ascherson calls the primary root, he terms an adventitious root.

Murbeck agrees with Wille and in further investigations finds that the primary root rudiment "sich eben am Festpunkte des Embryos, mit anderen Worten, eben am Platze der Radicula befindet. Dass dieselbe wirklich die Anlage der Radicula repräsentiert, kann wohl schwerlich bezweifelt werden" (1902, p. 17).

That the adventitious root is of exogenous origin is explained by Wille (1883, p. 5) and defended by Murbeck (l. c. p. 18) by the fact that practically all of the cells of the young embryo are meristematic, so that an adventitious root developing at this period may easily have an exogenous origin.

My own slides testify to the correctness of the interpretations and figures of Wille and Murbeck. Nowhere is there the least evidence that the hypocotyl is the "seitliche Auftreibung" described by Ascherson, and there seems no doubt but that the root near the base of the epicotyl is properly the first adventitious root, which

has assumed the function of the primary root of the embryo. Such an adventitious root, we have seen, may occur in a similar way at any node in the mature plant, just below the point of leaf-insertion.

Just what the group of cells at the base of the hypocotyl does represent is difficult to say definitely. Murbeck thinks that they may represent calyptrogen and calyptra (1902, p. 18). This is, of course, possible, but it would be difficult to prove. We may be sure of this much, however, that from their position, appearance, and development, they bear some relation to the now functionless primary root.

Another interpretation of this whole thickened hypocotyl with its curious basal cells seems plausible, namely, that practically the whole swollen area itself represents the primary root or radicle which has been by degrees metamorphosed into a storage-organ. That this is actually what has happened would be difficult to prove, for it is dangerous to lay much stress on the form and position of the storage organs. The strongest grounds for such an opinion are drawn from a comparative morphological study. The embryo of Zannichellia, e. g., is very similar to that of Ruppia. Although Wille considers (1883, p. 7) that the small caplike body at the base of the hypocotyl comprises the entire root, Campbell's figures and description (1897, pp. 50, 51 and Pl. V, figures 120, 122, 123) go to show that practically the whole hypocotyl is a root structure and the small body at its base is the root cap.

In Zannichellia the primary root functions for a time during germination (Wille, 1883, p. 8). The absence of a distinct plerome and periblem in what has been called the hypocotyl of Ruppia may be accounted for by the degeneration of this tissue, its assumption of the function of storage, and the transfer of its functioning power as a root to the adventitious root.

FRUIT AND SEED

Pl. IV, fig. 13 shows a cluster of mature fruits, and, as may be seen, the form varies somewhat, but is always bluntly pointed at the apex, with a one-sided base, the whole being slightly oblique with respect to the axis of the stipe. At the maturity of the fruit, the stigma generally drops off, leaving the blunt apex shown in the figure.

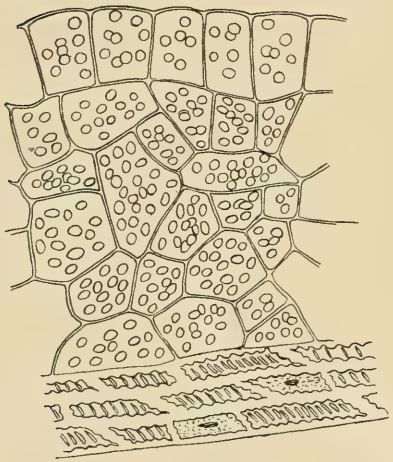


Figure 30.—Section through ovary wall of ripe fruit, showing the three innermost hardened layers, which form the covering of the seed, and the outer soft parts. × 210.

Figure 31.—Two ripe achenes, after disintegration of the outer soft parts of the fruit covering; showing the pronounced beaks. × 35.

During the development of the seed, changes occur in the wall of the ovary, the most important of which is the thickening of the cell-walls of portions contiguous to the seed, with the result that this inner layer of the ovary-wall becomes quite hard. This hardened portion is limited to about three layers of cells. Outside of this hard layer are about five or six layers of thin-walled cells, copiously supplied with starch, and these, in turn, are bounded by the epidermis, also rich in starch (Text-fig. 30).

The ripened fruit has a greater specific gravity than water, which one can easily demonstrate by breaking off the fruit from the stipe. It then sinks immediately to the bottom, and, in most cases, probably passes the winter embedded in the mud. Under such conditions, the outer soft parts of the fruit-covering soon decay, leaving the inner thickened portion of the ovary-wall which surrounds the seed. Since this area extends up into the stylar canal, the result is an appearance as in Text-fig. 31. At the end is a long beak, derived from the stylar region. Such a structure is accordingly an achene, its outer layer being hard, dry and indehiscent, and derived from the ovary.

A prominent beak is supposed to be a specific character of *Ruppia rostellata*. But a comparison with the figures of Irmisch (1858) of *R. rostellata* demonstrates that the beak represented there is not any longer than that of my specimens, although of a slightly different shape.

A similar development of fruit and seed is indicated by Campbell (1897) in Zannichellia, where a seed is formed surrounded by a pericarp from the ovary-wall. Such achenes are also well known to occur in the grasses.

SEEDLING

Germination. A considerable number of seeds were germinated in the laboratory. Seeds gathered in October, at the end of the flowering season, first began to germinate in December, and from that time on seedlings appeared intermittently. It is evident, therefore, that the seed requires a short period of rest before the new growth begins.

Seedlings were grown either in mud from their native habitat, or in clean-washed sand, the latter being preferable, on account of the numerous algae, bacteria, &c. which soon develop in the former. The salt water used was taken from New Haven Harbor.

Irmisch (1858) noticed in the achene of *Ruppia rostellata* a small, slightly swollen, elongated area which he claimed was the place of exit for the cotyledon and root on germination. Such a spot occurs also in *Ruppia maritima*, but I have been unable to ascertain definitely if this is the region which is ruptured at germination. In most cases a more or less triangular area of the hard, dark-brown covering is pushed off and the cotyledon and adventitious root make their appearance (Pl. XV, fig. 120). In figure 121 the whole pericarp has been purposely removed to show the enormous hypocotyl.

Figure 120 shows a seedling about three days old. Here the three vegetative organs are disclosed: the first foliage leaf is developed from the cotyledon, which becomes green; the stem is formed by the elongation of the hypocotyl; and the root grows rapidly downward, becoming abundantly furnished with root-hairs.

In the case of the root, it is interesting to note that it exhibits a general tendency to first grow upwards for a short time, only later turning downward. The proportional growth of roots and leaves seems to vary considerably (Pl. XV, figs. 120, 121).

Formation of Rootstock. Text-figs. 32 and 33 are drawings—natural size—of seedlings grown in the laboratory in washed sand and harbor water. The seeds were collected in January, being extracted from mud taken from the bottom of a ditch where *Ruppia maritima* grows and fruits abundantly, many of the parent plants being even at that time in a green, flourishing condition. On being placed in a warm room, germination occurred in a few days.

During their growth the young plants showed very clearly the manner in which the horizontal rootstock is developed. At first the seedling is erect, but soon, as it increases in length, reclines

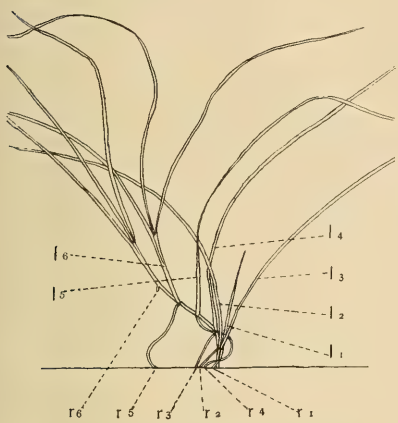


Figure 32.—Young seedling, showing development of horizontal rootstock. *l1*, *l2*, *l3*, &c., successively older leaves; *r1*, *r2*, *r3*, &c., successively older adventitious roots. ½ natural size

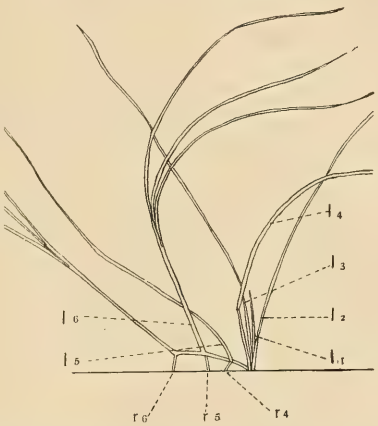


Figure 33.—Young seedling, older than preceding one, showing more advanced development of horizontal rootstock. Abbreviations as in previous figure. ½ natural size.

somewhat, and at the same time an adventitious root (Text-fig. 32, r_1) appears at the first node and grows downward, fixing itself in the soil or sand. This is repeated at successive nodes, the shoot reclining more and more, and Text-fig. 32 shows an advanced stage where five adventitious roots have been developed, and a sixth (r_6) is just appearing. Three days after the drawing was made, this sixth root had reached the surface of the sand. In this figure the roots have almost the appearance of drawing down the stem to a horizontal position. Whether or not this is actually the case, a horizontal location is ultimately attained, as in Text-fig. 33. Here, indeed, the first roots have apparently drawn the oldest part of the seedling well down into the sand.

From this time on the seedling assumes the habit of the mature plant. From the nodes upright shoots may arise, which may also develop later in the same way into root stocks, thus forming a branched rootstock; or it is conceivable that these upright shoots may continue in an erect position, ultimately reaching the surface of the water and flowering.

The anatomy of the seedling corresponds in the main to that of the mature plant. The central vascular area in the stem is thus essentially the same as in the older plant, so that no ancestral characters were detected in the vascular system in this young stage.

SUMMARY OF PARTS ON REPRODUCTIVE ORGANS, EMBRYO, &c.

Flower. The inflorescence is spadix-like, and even a small spathe is present, the latter structure having almost entirely escaped the notice of investigators.

The small scaly outgrowths from the anther-connective probably represent reduced floral leaves, judging from the analogy of Potamogeton, and from the fact that the flower of Ruppia is evidently a reduced one.

The two flowers of the spadix arise laterally from the vegetative cone; they develop practically together in point of time, and the anthers precede the pistils in development.

Microsporangium. Appearances indicate that the archesporial initials in the microsporangium are a comparatively large group of cells which originate simultaneously both in plerome and periblem.

A plate of sporogenous cells becomes differentiated to form the future septum dividing the two sacs of the theca.

The tapetum is evidently derived from the sporogenous cells.

The sporophytic number of chromosomes was definitely ascertained to be sixteen.

Megasporangium. The megasporangium arises from a hypodermal cell in the usual way. Generally one layer of parietal cells is formed.

An interesting case was found of two megaspore mother-cells in one megasporangium, a condition little known among monocotyledons.

Female Gametophyte. Eight chromosomes appear in the first reduction division, and probably in the succeeding ones.

A double megaspore mother-cell was found, which had in each case divided into two daughter-cells.

The four potential megaspores are oriented in such a way that the two outer cells are in contact with the third cell, but separated by it from the innermost cell.

The embryo-sac develops in the usual way and always from the innermost potential megaspore, the outer ones becoming resorbed. The antipodal cells are surrounded by cytoplasm and a thin membrane, and are always three in number. No further divisions among them were observed.

Male Gametophyte. The tetrads are oriented to each other like the four quadrants of a sphere.

Eight chromosomes appear in the reduction-division.

The generative cell is formed very early in the development, at the end of the young pollen-grain. No membrane now or later separates it from the rest of the grain.

When the grain has nearly reached maturity, the generative cell divides, the two resulting male cells remaining united.

The mature pollen-grain is of peculiar shape, but similar forms occur in other Potamogetonaceae.

The wall of the pollen-grain is formed inside of the walls of the tetrads, these latter walls becoming apparently dissolved.

The wall is never of more than a single layer. The thickenings on its exterior appear to be the result of depositions. At certain regions these depositions are omitted, and these spots are probably the places where the pollen-tube may commence its formation.

Pollination. Pollination is accomplished by means of water, an unusual method.

Endosperm. The endosperm is scanty, never more than a thin layer lining the embryo-sac, and containing free nuclei.

Embryo. The suspensor is limited to a single large cell, which later develops to an enormous size.

The embryo evidently develops from two or three primary segments as in the typical monocotyledonous embryo.

An unusual state of affairs exists, however, in the large number of early longitudinal divisions.

Apparently both cotyledon and stem-apex arise from the terminal segment as in Zannichellia, but this cannot be definitely proved, on account of the obscurity of the segment boundaries.

The two lower segments form hypocotyl, adventitious root, and primary root.

I agree with Murbeck in locating the vestiges of the primary root at the base of the enlarged hypocotyl.

Another possible interpretation is that practically the whole swollen area is a root, metamorphosed into a storage organ.

Seed and Fruit. The fruit is an achene, the hard coat being derived from the inner portion of the ovary wall.

Seedling. At germination the cotyledon develops chlorophyll, and the adventitious root of the embryo is the first functioning root.

At first the young seedling is upright, but very soon a horizontal root-stock is developed.

SUMMARY OF RELATIONSHIPS TO OTHER POTAMOGETONACEAE.

On account of the incomplete knowledge we have at present of the members of the Potamogetonaceae, a thorough comparison with them in all points of gross morphology and of anatomy is of course impossible. In the course of this paper I have from time to time alluded to the points of likeness and difference with respect to the remaining Potamogetonaceae, as far as I have been able to glean such from the various articles cited. It is my purpose now to briefly review these here, touching upon the various characters in the order pursued in my paper.

As regards the methods of branching, Cymodocea, Phyllospadix, and Zostera most resemble Ruppia, with a monopodial system in the rootstock and its branches, and a sympodial inflorescent system.

In stem anatomy, perhaps *Potamogeton pectinatus* and *Zostera marina* resemble Ruppia most closely, while Zannichellia and Althenia are also very similar in all respects except that they lack the cortical bundles. The evidence here seems to point to the conclusion that Zostera and Potamogeton are more primitive genera, while, on the other hand, Zannichellia and Althenia are more reduced, with Ruppia somewhere between.

The leaf of Ruppia shows a great similarity in external form to certain species of Potamogeton and to Zannichellia and Althenia. I do not find the secretion cells of the leaf—or indeed of any part of the plant—reported for any but Cymodocea, Posidonia, and Halodule, besides Ruppia. In other points of anatomy, however, the leaf of *Potamogeton pectinatus* is very similar, while the leaves of Zannichellia and Althenia show a strong resemblance, but with absence of the lateral bundles. The natural conclusion based on this evidence is, as stated before, that Ruppia is descended from some form similar to the present submerged Potamogetons, and also that Zannichellia and Althenia are still further reduced.

In the root system, although Ruppia has usually only one root at each node, Zannichellia and Althenia have two, and the Potamogetons several, even *Potamogeton pectinatus* developing four or more (Irmisch, 1858). In Zostera and Phyllospadix a cluster of roots occurs at the nodes. The coleorrhiza has been reported in Potamogeton, Zannichellia, and Cymodocea, and probably occurs also in Althenia and Zostera. In the root anatomy, *Potamogeton pectinatus*, Zannichellia and Althenia correspond closely with Ruppia, as is the case in the other vegetative organs, Zannichellia showing the four distinct meristematic regions at the growing-point as in Ruppia.

Passing to the reproductive organs, where, owing to our lack of information, the comparison is most unsatisfactory, we have seen that the inflorescence is spadix-like, resembling Potamogeton and Zostera, and that the flowers themselves are apparently reduced from some form like Potamogeton.

The archesporium of the microsporangium probably arises in Zannichellia in much the same way as in Ruppia, i. e., originating simultaneously from a large group of cells. Only one species of Potamogeton has been investigated on this point, and here the archesporium is traceable to a single hypodermal cell. Like Ruppia, Zostera also derives tapetum from the outer sporogenous cells, but *Potamogeton foliosus* differentiates it from the wall.

Parietal tissue exhibits a much greater development in the megasporangium of Potamogeton than in Ruppia, and in this respect Zannichellia probably more closely resembles Ruppia. This consideration again points to Potamogeton as the more primitive form. In *Potamogeton natans* (p. 138) an arrangement of the potential megaspores has been found such as occurs in Ruppia.

The pollen-grains of Zannichellia and Potamogeton are more or less globular, those of Ruppia somewhat elongated, while those of Zostera and Phyllospadix have attained extreme length so that they might be termed filamentous. These differences depend presumably on the different modes of pollination prevailing among these genera.

More than any other member of the Potamogetonaceæ so far investigated, the embryo of Zostera has points in common with Ruppia in the manner of its development, and, as is the case with the mature embryo of Zannichellia, resembles it in its mature form. The primary root of Zostera, however, functions for a time during germination.

It will be seen from these considerations that, on the whole,

Ruppia is closer to Potamogeton, Zannichellia, and Althenia than to any others of the Potamogetonaceae, especially with regard to the vegetative organs; and yet, in its embryo, it most strongly resembles Zostera. Similarities in the vascular structure of the vegetative organs are looked upon generally as comparatively fixed indications of relationship; so that in this case the evidence points to Ruppia as being derived from some form similar to the present submerged Potamogetons, with Zannichellia and Althenia serving as examples of still further reduction.

BIBLIOGRAPHY

1. Andrews, F. M., 1895. Development of the Embryo-sac of *Jeffersonia diphylla*. Bot. Gaz. **20**: 423–424. pl. 28.
2. Ascherson, P., 1889. Potamogetonaceae. In Engler and Prantl's Die natürlichen Pflanzenfamilien. **2**[1]: 194–214. figures 152–164. Leipzig.
3. Atkinson, G. F., 1905. A College Textbook of Botany. New York.
4. Bernard, Ch., 1900. Recherches sur les Sphères attractives chez *Lilium candidum*, &c. Jour. Bot. **14**: 118–124, 177–188, 206–212. pls. 4–5.
5. Bornet, E., 1864. Recherches sur le *Phucagrostis major* Cavol. Ann. Sci. Nat. Bot. V. **1**: 5–51. pls. 1–11.
6. Bower, F. O., 1897. Studies in the Morphology of Spore-producing Members. III. Marattiaceae. Phil. Trans. Roy. Soc. London. Bot. **189**: 35–81. pls. 7–11.
7. Britton, N. L., 1907. Manual of the Flora of the Northern States and Canada. Third Edition. New York.
8. Britton, N. L., and Brown, A., 1898. An Illustrated Flora of the Northern United States and Canada. 3 vols. New York.
9. Caldwell, O. W., 1899. On the Life-History of *Lemna minor*. Bot. Gaz. **27**: 37–66. figures 1–59.
10. Campbell, D. H., 1897. A Morphological Study of Naias and Zannichellia. Proceedings of the Cal. Acad. of Sciences. III. Bot. **1**: 1–61. pls. 1–5.
11. —— —— 1898. The Development of the Flower and Embryo in *Lilaea subulata*, H. B. K. Ann. of Bot. **12**: 1–28. pls. 1–3.
12. —— —— 1899. Notes on the Structure of the Embryo-sac in Sparganium and Lysichiton. Bot. Gaz. **27**: 153–166. pl. 1.
13. Caspary, R., 1858. Die Hydrilleen. Jahrb. Wiss. Bot. **1**: 377–513. pls. 25–29.
14. Čelakovský, L. J., 1896. Über den phylogenetischen Entwicklungsgang der Blüte und über den Ursprung der Blumenkrone. I. Sitzber. Königl. Böhm. Gesell. Wiss. 1896[40]: 1–91. figures 1–4.
15. —— —— 1900. Über den phylogenetischen Entwicklungsgang der Blüte und über den Ursprung der Blumenkrone. II. Sitzber. Königl. Böhm. Ges. Wiss. 1900[3]: 1–221. figures 1–30.
16. Chamberlain, C. J., 1905. Methods in Plant Histology. Second Edition. Chicago.
17. Chrysler, M. A., 1907. The Structure and Relationships of the Potamogetonaceae and Allied Families. Bot. Gaz. **44**: 161–188. pls. 14–18.
18. Coulter, J. M., 1898. Contribution to the Life-History of Ranunculus. Bot. Gaz. **25**: 73–88. pls. 4–7.

19. Coulter, J. M., and Chamberlain, C. J., 1903. Morphology of Angiosperms. New York.
20. De Bary, A., 1884. Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns. Transl. by F. O. Bower and D. H. Scott. Oxford.
21. Douliot, H., 1890. Recherches sur la Croissance terminale de la Tige des Phanérogames. Ann. Sci. Nat. Bot. VII. **11**: 283–350. pls. 13–19.
22. Dudley, W. R., 1893. The Genus Phyllospadix. Reprinted from the Wilder Quarter-Century Book. 403–420. pls. 1—2. Ithaca, N. Y.
23. Eichler, A. W., 1865. Zur Entwicklungsgeschichte des Blattes mit besonderer Berücksichtigung der Nebenblatt-Bildungen. Marburg.
24. —— —— 1875. Blütendiagramme. 2 vols. Leipzig.
25. Fischer, A., 1880. Zur Kenntniss der Embryosackentwicklung einiger Angiospermen. Jenaische Zeitsch. Naturwiss. **14**: 90–132.
26. Flahault, Ch., 1878. Recherches sur l'Accroissement terminal de la Racine chez les Phanérogames. Ann. Sci. Nat. Bot. VI. **6**: 1–168. pls. 1–8.
27. Ganong, W. F., 1903. The Vegetation of the Bay of Fundy Salt and Diked Marshes: an Ecological Study. Bot. Gaz. **36**: 161–186, 280–302, 349–367, 429–455. figures 1–16.
28. Goebel, K., 1893. Pflanzenbiologische Schilderungen. Marburg.
29. —— —— 1898. Organographie der Pflanzen. Jena.
30. Griffith, W., 1851. I. Notulae ad Plantas Asiaticas. Part. III. Monocotyledonous Plants. Calcutta.
31. —— —— 1851. II. Icones Plantarum Asiaticarum. Part. III. Monocotyledonous Plants. Calcutta.
32. Grönland, J., 1851. Beitrag zur Kenntniss der *Zostera marina* L. Bot. Zeit. **9**: 185–192. pl. 4.
33. Guignard, L., 1882. Recherches sur le Sac embryonnaire des Phanérogames Angiospermes. Ann. Sci. Nat. Bot. VI. **13**: 136–199. pls. 3–7.
34. Haberlandt, G., 1896. Physiologische Pflanzenanatomie. Second Edition. Leipzig.
35. Hansgirg, A., 1903. Phyllobiologie. Leipzig.
36. Hegelmaier, F., 1870. Über die Entwicklung der Blütenteile von Potamogeton. Bot. Zeit. **28**: 281–289, 313–319. pl. 5.
37. Hillebrand, W., 1888. Flora of the Hawaiian Islands. New York and London.
38. Hofmeister, W., 1852. Zur Entwickelungsgeschichte der Zostera. Bot. Zeit. **10**: 121–131, 137–149. pl. 3.
39. Hofmeister, W., 1861. Neue Beiträge zur Kenntniss der Embryobildung der Phanerogamen. II. Monocotyledonen. Abh. d. K. Sächs. Gesell. der Wiss. **7**: 631–760. pls. 1–25.
40. Holferty, G. M. 1901. Ovule and Embryo of *Potamogeton natans*. Bot. Gaz. **31**: 333–346. pls. 2, 3.

41. Holm, T., 1905. Studies in the Gramineae: VIII. *Munroa squarrosa.* (Nutt) Torr. Bot. Gaz. **39**: 123–136. figures 1–12.
42. Hooker, J. D., 1894. The Flora of British India. VI. Orchideae to Cyperaceae. London.
43. Irmisch, Th., 1851. Über die Inflorescenzen der deutschen Potameen. Flora **34**: 81–93. 1 pl.
44. —— —— 1858. Über einige Arten aus der natürlichen Pflanzenfamilie der Potameen. Abhandl. des naturwiss. Vereines für die Provinz Sachsen und Thüringen. **2**: 1–56. pls. 1–3. Berlin.
45. Juel, H. O., 1884. Beiträge zur Kenntniss der Hautgewebe der Wurzeln. Bihang till K. Svenska Vet.-Akad. Handlingar. $\mathbf{9}^{9}$: 1–18. pls. 1–2.
46. Lachmann, P., 1906. Origine et Développement des Racines et des Radicelles du *Ceratopteris thalictroides.* Ann. Univ. Grenoble. $\mathbf{18}^{2}$: 1–39.
47. Leavitt, R. G., 1902. The Root Hairs, Cap, and Sheath of Azolla. Bot. Gaz. **34**: 414–419. pl. 16.
48. —— —— 1904. Trichomes of the Root in Vascular Cryptogams and Angiosperms. Proc. Boston Soc. Nat. Hist. **31**: 273–313. pls. 16–19.
49. Magnus, P., 1870. Beiträge zur Kenntniss der Gattung Najas L. Berlin.
50. Massart, J., 1894. La Récapitulation et l'Innovation en Embryologie végétale. Bull. Soc. Roy. Bot. Belgique $\mathbf{33}^{1}$: 150–247. figures 1–54. pls. 1–4.
51. Morong, T., 1893. The Naiadaceae of North America. Mem. Torr. Bot. Club. $\mathbf{3}^{2}$: 1–65. pls. 1–74.
52. Mottier, D. M., 1895. Contributions to the Embryology of the Ranunculaceae. Bot. Gaz. **20**: 241–248, 296–304. pls. 17–20.
53. Müller, F., 1877. Untersuchungen über die Struktur einiger Arten von Elatine. Flora **60**: 481–496, 519–525. pl. 7.
54. Murbeck, S. V., 1902. Über die Embryologie von *Ruppia rostellata* Koch. K. Svenska Vet.-Akad. Handl. $\mathbf{36}^{5}$: 1–21. pls. 1–3.
55. Pechoutre, F., 1902. Contribution à l'Etude du Développement de l'Ovule et de la Graine des Rosacées. Ann. Sci. Nat. Bot. VIII. **16**: 1–158. figures 1–166.
56. Pond, R. H., 1905. The Biological Relation of Aquatic Plants to the Substratum. Report of U. S. Fish Commission **1903**: 483–526. figures 1–6, with tables.
57. Prantl, K., 1883. Studien über Wachstum, Verzweigung und Nervatur der Laubblätter, insbesondere der Dikotylen. Ber. Deutsch. Bot. Gesell. **1**: 280–288.
58. Prillieux, E., 1864. Recherches sur la Végétation et la Structure de *l'Althenia filiformis* Petit. Ann. Sci. Nat. Bot. V. **2**: 169–190. pls. 15–16.
59. Rosenberg, O., 1901. I. Über die Embryologie von *Zostera marina.* Bih. till K. Svensk. Vetensk. Akad. Handl. $\mathbf{27}^{6}$: 1–24. pls. 1–2.

60. Rosenberg, O., 1901. II. Über die Pollenbildung von Zostera. Meddel. Stockholms Högsk. Bot. Inst.: 1–21.
61. Roze, E., 1894. Recherches sur les Ruppia. Bull. de la Soc. Bot. de France. **41**: 466–480. pl. 5.
62. Sachs, J., 1875. A Textbook of Botany. English Edition. Oxford.
63. —— —— 1887. Lectures on the Physiology of Plants. English Edition. Oxford.
64. Sauvageau, C., 1889. Contribution à l'Etude du Système mécanique dans la Racine des Plantes aquatiques: Zostera, Cymodocea et Posidonia. Extr. du Journal de Botanique. 1889: 169–181. figures 1–5.
65. —— —— 1891. I. Sur la Tige des Zostera. Jour. de Bot. V: 33–45, 59–68. figures 1–9. (Ref. in Just's Bot. Jahresb. 1891, I, p. 615.)
66. —— —— 1891. II. Sur les Feuilles de quelques Monocotylédones aquatiques. Ann. Sci. Nat. Bot. VII. **13**: 103–296. figures 1–64.
67. Schaffner, J. H., 1896. The Embryo-sac of *Alisma Plantago*. Bot. Gaz. **21**: 123–132. pls. 9–10.
68. —— —— 1897. I. The Development of the Stamens and Carpels of *Typha latifolia*. Bot. Gaz. **24**: 93–102. pls. 4–6.
69. —— —— 1897. II. Contribution to the Life-History of *Sagittaria variabilis*. Bot. Gaz. **23**: 252–273. pls. 20–26.
70. Schenck, H., 1886. Vergleichende Anatomie der submersen Gewächse. Bibliotheca Bot. **1**: 1–67. pls. 1–10.
71. Schilling, A. J., 1894. Anatomisch-biologische Untersuchungen über die Schleimbildung der Wasserpflanzen. Flora **78**: 280–360.
72. Schimper, A. F. W., 1890. Über Schutzmittel des Laubes gegen Transpiration, besonders in der Flora Java's. Sitzb. Akad. Berlin, 1890: 1045–1062.
73. —— —— 1891. Die indo-malayische Strandflora. Bot. Mitteilungen aus den Tropen. **1**[3]: 1–204. pls. 1–7.
74. —— —— 1898. Pflanzengeographie auf physiologischer Grundlage. Jena.
75. Schumann, K., 1892. Morphologische Studien. I. Leipzig.
76. Scott, Daisy G., 1906. The Apical Meristems of the Roots of Certain Aquatic Monocotyledons. The New Phytologist. **5**: 119–129, pl. 9.
77. Scott, D. H., 1894. Recent Work on the Morphology of Tissues in the Higher Plants. Science Progress. **1**: 463–482.
78. Snow, Laetitia M., 1905. The Development of Root Hairs. Bot. Gaz. **40**: 12–48. pl. 1.
79. Solms-Laubach, H. Graf zu, 1878. Über monocotyle Embryonen mit scheitelbürtigem Vegetationspunkt. Bot. Zeit. **36**: 65–74, 81–93. pl. 4.
80. Strasburger, E., 1873. Über Azolla. Jena.
81. —— —— 1879. Die Angiospermen und die Gymnospermen. Jena.
82. —— —— 1882. Über den Bau und das Wachstum der Zellhäute. Jena.

83. Strasburger, E., 1889. Über das Wachstum vegetabilischer Zellhäute. Histol. Beitr. **2**. Jena.
84. —— —— 1891. Über den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen. Histol. Beitr. **3**. Jena.
85. Strasburger, Noll, Schenck u. Karsten, 1908. Lehrbuch der Botanik. Ninth Edition. Jena.
86. Treub, M., 1876. Le Méristème primitif de la Racine dans les Monocotylédones. Leyden.
87. Tyler, A. A., 1898. The Nature and Origin of Stipules. Ann. of N. Y. Acad. of Sci. **10**: 1–49. pls. 1–3.
88. Van Tieghem, Ph., 1870–1871. Recherches sur la Symétrie de Structure des Plantes vasculaires. Ann. Sci. Nat. Bot. V. **13**: 5–314. pls. 3–8.
89. —— —— 1898. Eléments de Botanique. 2 vols. Paris.
90. Vines, S. H., 1898. An Elementary Text-Book of Botany. London and New York.
91. Ward, H. Marshall, 1880. A Contribution to our Knowledge of the Embryo-sac in Angiosperms. Jour. Linn. Soc. Bot. London. **17**: 519–546. pls. 17–25.
92. Warming, E., 1873. Untersuchungen über pollenbildende Phyllome und Kaulome. Hanstein's Bot. Abhandl. **2**[2]: 1–90. pls. 1–6.
93. Warming, E., 1902. Lehrbuch der ökologischen Pflanzengeographie. Second German Edition. Berlin.
94. Watson, S., 1890. Miscellaneous Notes upon North American Plants, chiefly of the United States, with Descriptions of New Species. Proc. of Am. Acad. of Arts and Sci. **25**: 124–140.
95. Wiegand, K. M., 1899. The Development of the Microsporangium and Microspores in Convallaria and Potamogeton. Bot. Gaz. **28**: 328–359. pls. 24–25.
96. —— —— 1900. The Development of the Embryo-sac in some Monocotyledonous Plants. Bot. Gaz. **30**: 25–47. pls. 6–7.
97. Wille, N., 1883. Om Kimens Udviklingshistorie hos *Ruppia rostellata* og *Zannichellia palustris*. Videnskabelige Meddelelser fra d. naturhist. Forening i Kjøbenhavn. 1882–6: 1–14. pls. 1–2.
98. Wylie, R. B., 1904. The Morphology of *Elodea canadensis*. Bot. Gaz. **37**: 1–22. pls. 1–4.

EXPLANATION OF PLATES

Abbreviations. *A* & *B*, primary segments of embryo; *adr*, adventitious root; *ant*, antipodal cells; *as*, axillary scale; *ax*, axillary member; *axb*, axial bundle; *axbr*, axillary branch; *C*, third segment of embryo; *c*, cortex; *cal*, calyptrogen; *cb*, cortical bundle; *cc*, companion cell; *col*, coleorrhiza; *con*, connective; *cot*, cotyledon; *d*, dermatogen; *di*, diaphragm; *e*, egg; *ems*, embryo-sac; *end*, endodermis; *ep*, epidermis; *epc*, epicotyl; *fl*, flower; *fsl*, floral scale leaf; *gen* generative cell; *GP* or *gp*, growing point; *hyp*, hypocotyl; *i*, intercellular space; *ic*, inner cortex; *la*, lacuna; *L* or *l*, leaf; *lb*, lateral bundle; *low. sfl*, lower subfloral leaf; *lpn*, lower polar nucleus; *ma*, male cells; *mc*, middle cortex; *oc*, outer cortex; *pa*, parietal layer or layers; *pb*, periblem; *ped*, peduncle; *pist*, pistil; *pl*, plerome; *pm*, pollen mother-cells; *pr*, primary root cells; *r*, root; *rh*, root hairs; *rha*, rhachis; *rs*, root stock; *s*, sieve tube; *se*, secretion cells; *sfl*, subfloral leaf; *sg*, starch-grains; *sh*, sheath; *spo*, sporogenous cells; *spt*, septum; *st*, stem or stem apex; *sta*, stamen; *stc*, stylar canal; *stg*, stigma; *sti*, stipe; *sus*, suspensor; *syn*, synergidae, *ta*, tapetum; *th*, theca; *tn*, tube nucleus; *tra*, tracheae; *tri*, trichoblasts; *u*, undulations; *upn*, upper polar nucleus; *up. sfl*, upper subfloral leaf; *ust*, upright stem; *vsl*, vegetative scale leaf.

PLATE I

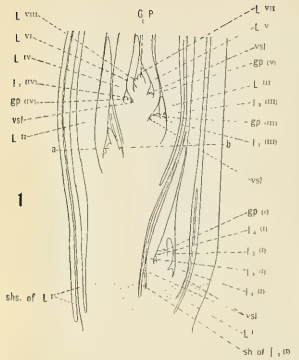
Figure 1.—Longitudinal section of stem-apex, showing growing-point and manner of development of leaves and axillary buds; L^{I}, L^{II}, L^{III}, &c., primary leaves; $l_1^{(I)}$, $l_2^{(I)}$, &c., $l_1^{(II)}$, $l_2^{(II)}$, &c., leaves of axillary buds of L^{I}, L^{II}, &c.; *G P*, main growing-point of stem; $gp^{(V)}$, $gp^{(IV)}$, &c., growing-points of axillary buds; *ab*, line where such a cross section as is represented in Plate VII, figure 43, might be cut perpendicular to plane of paper. × 30.

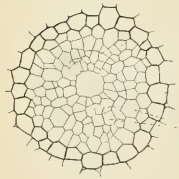
Figure 2.—Sketch from living specimen, showing vegetative branch system in a young stage; *I, II, III, IV,* &c., primary leaves. ½ natural size.

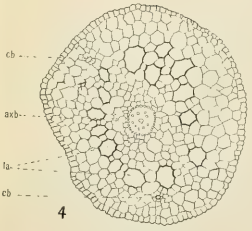
Figure 3.—Cross section of axial bundle of stem, showing endodermis, sieve tubes, central cavity formed by disorganization of tracheae, &c. × 300.

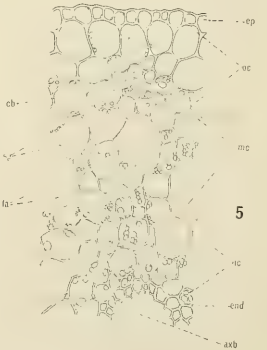
Figure 4.—Cross section of stem. × 60.

Figure 5.—Cross section of epidermis, cortex and endodermis of stem. × 212.









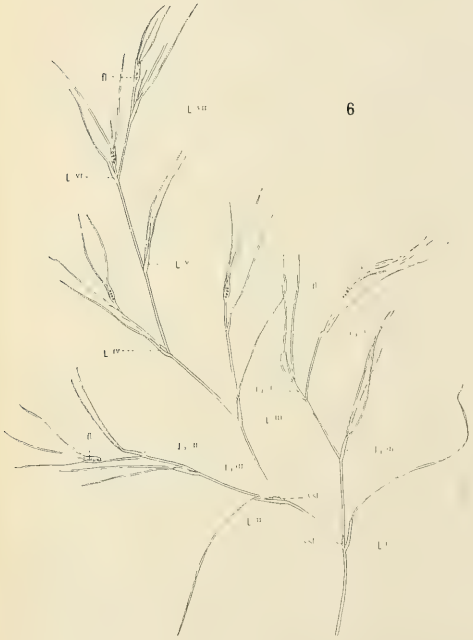


PLATE II

Figure 6.—Sketch from living specimen, showing vegetative branch system in a mature stage, just previous to the appearance of flowers. Abbreviations as in figure 1. $\frac{1}{2}$ natural size.

PLATE III

Figure 7.—Photomicrograph of cross section of stem, showing axial bundle, endodermis, cortex, lacunae, and epidermis. × 30.

Figure 8.—Photomicrograph of cross section of stem, axillary bud and subtending leaf; showing axillary scales, vegetative scale leaf surrounding axillary bud, secretion cells, &c. × 25.

Figure 9.—Photomicrograph of cross section of rootstock; showing axial bundle, endodermis, cortex, lacunae, cortical bundles, epidermis, and starch-grains in cortex. × 50.

Figure 10.—Photomicrograph of cross section through node of rootstock; showing two roots developing, and epidermis of rootstock over each root becoming meristematic. × 35.

Figure 11.—Photomicrograph of cross section through rhachis; showing axial bundle with lacunae, &c., and surrounding stamen, with its two thecae, connective, &c. × 35.

Figure 12.—Photomicrograph of longitudinal section through end of rhachis; showing its blunt apex and various sections of pistils and anthers. × 35.

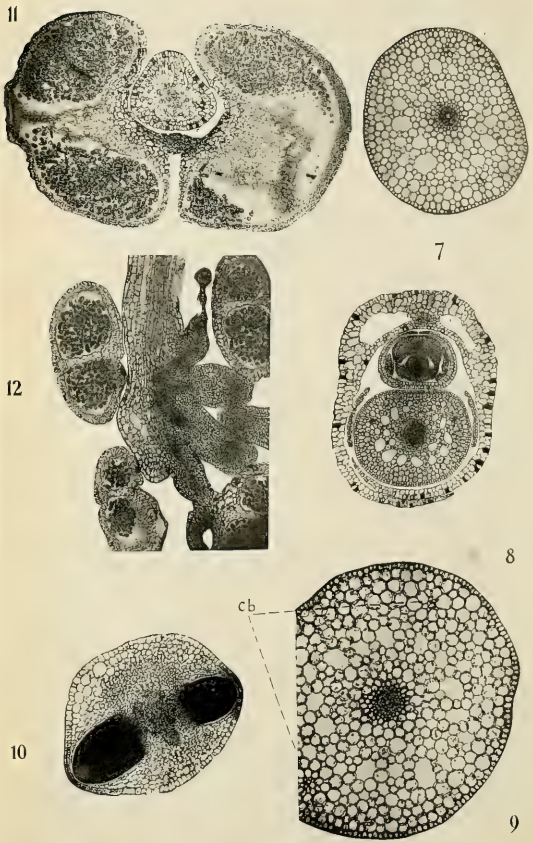


PLATE IV

Figure 13.—Drawing of cluster of fruit about mature. × 5.

Figure 14.—Surface view of epidermis of stipe (young stage); showing secretion cells. × 212.

Figure 15.—Cross section of mature stipe; showing epidermis, cortex, and axial bundle; intercellular spaces and lacunae stippled; x = apparently halved epidermal cells. × 185.

Figure 16.—Part of cross section of stipe, showing strengthened epidermis, part of cortex, lacunae and small intercellular spaces. × 212.

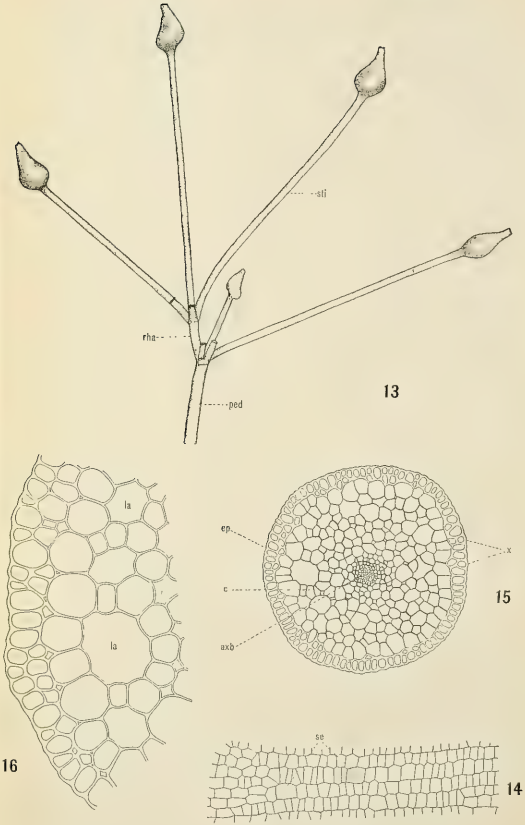
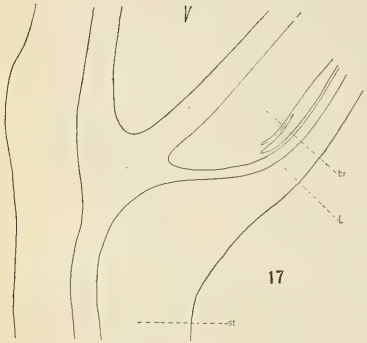


PLATE V

Figure 17.—Diagrammatic representation of median longitudinal section through stem and axillary branch; *L*, subtending leaf; vascular portions stippled. × 212.

Figure 18.—Diagrammatic representation of median longitudinal section through stem at base of inflorescent branch system, showing the course of the vascular bundles. Vascular portions stippled. × 212.

Figures 19–24.—A series of cross sections through stem beginning just below point of leaf insertion and extending up into leaf, showing course of cortical bundles from stem to leaf and independent origin of new cortical bundles in the stem. × 35.



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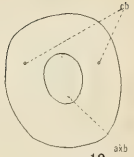

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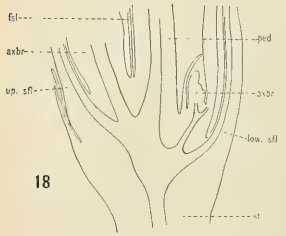

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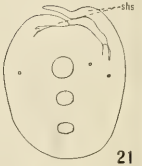

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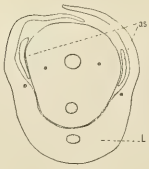

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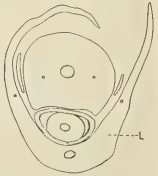

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PLATE VI

Figure 25.—Photomicrograph of longitudinal section through stem apex; showing growing point and leaves in successive stages of development, similarly as in Pl. I, fig. 1. × 40.

Figure 26.—Photomicrograph of apical portion of leaf, not quite mature; showing marginal teeth. × 35.

Figure 27.—Photomicrograph of cross section of root; showing epidermis, exodermis, cortex, endodermis and axial vascular bundle. × 60.

Figure 28.—Photomicrograph of young leaves surrounding growing-point, dissected from living specimen. × 35.

Figure 29.—Photomicrograph of portion of epidermis near apex of root; showing trichoblasts (the darkly stained cells). × 40.

Figure 30.—Photomicrograph of surface of leaf treated with a five per cent solution of potassium hydroxide; showing epidermal secretion cells and central vascular bundle. The marginal teeth have been worn off. × 30.

Figure 31.—Photomicrograph of a cross section through a node of the stem showing the origin of a single root—the typical condition. In this figure the meristematic layers at the growing point of the root are clearly defined. × 35.

Figures 32 and 33.—Photomicrographs of adjoining portions of a nearly median longitudinal section through the root apex, showing trichoblasts. (The root cap was slightly separated from the growing-point in preparation.) × 50.

Figure 34.—Photomicrograph of cross section of young peduncle, showing axial bundle, lacunae in cortex, &c. × 35.

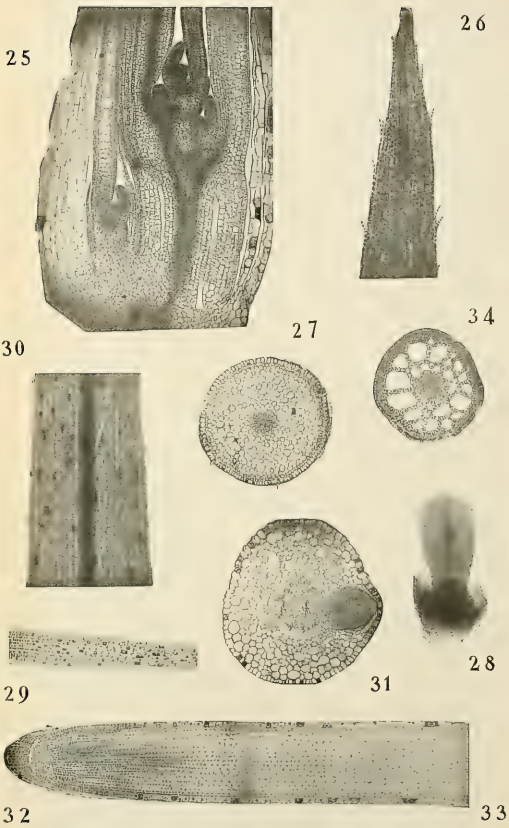


PLATE VII

Figure 35.—Sketch of flower bud; showing basal sheaths of subfloral leaves enclosing young flower. × 5.

Figure 36.—Sketch of portion of plant; showing horizontal rootstock and arrangement of roots and upright shoots. ½ natural size.

Figure 37.—Group of cells from vegetative scale leaf. × 162.

Figure 38.—Coleorrhiza from which young root has been forced out. × 10.

Figure 39.—Young leaf; showing teeth limited to extreme apex and comparatively large basal sheath. × 212.

Figure 40.—The vegetative scale leaf, detached, and flattened out. × 5.

Figure 41.—Longitudinal section through young inflorescence, showing floral scale leaf developing in connection with the flowers. × 20.

Figure 42.—Floral scale leaf *in situ*, close to young flowers. × 4.

Figure 43.—Cross section through vegetative bud, a little below the region of the growing point, cut at about the level shown by the line *ab* in figure 1. Abbreviations as in figure 1. The line *ab* in this figure represents the plane perpendicular to the paper, in which a longitudinal section such as is shown in figure 1 would lie. × 65.

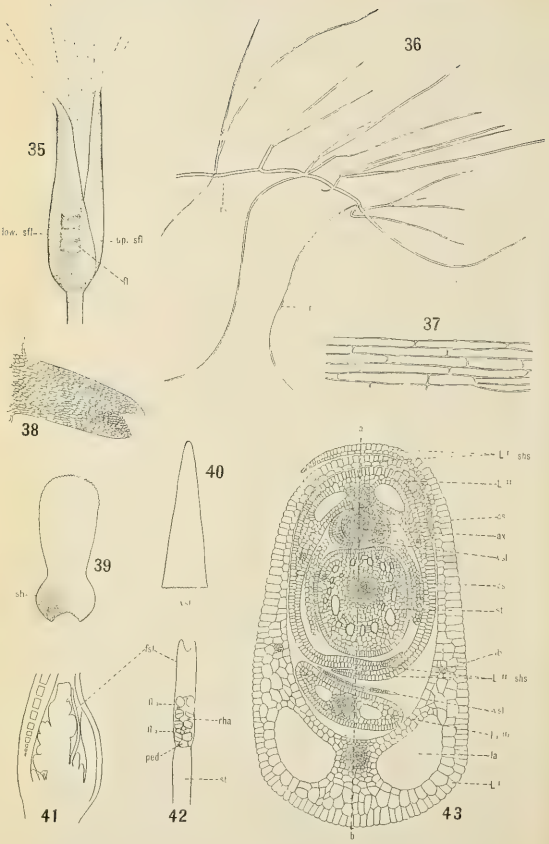


PLATE VIII

Figure 44. Longitudinal section of young root still enclosed in the stem; showing its origin in the stem, the meristematic epidermis and subepidermis in the stem above root apex and the four meristematic layers in the root. × 210.

Figure 45.—Portion of rootstock and root; the latter showing coleorrhiza. × 6.

Figure 46.—Cross section of vascular bundle of root with endodermis; showing tracheae and sieve tubes. × 400.

Figure 47.—Longitudinal section of vascular bundle of root, also with endodermis and, to the left, three layers of cortical parenchyma; showing tracheae, sieve tube, companion cell and undulations in walls of cortical parenchyma. × 400.

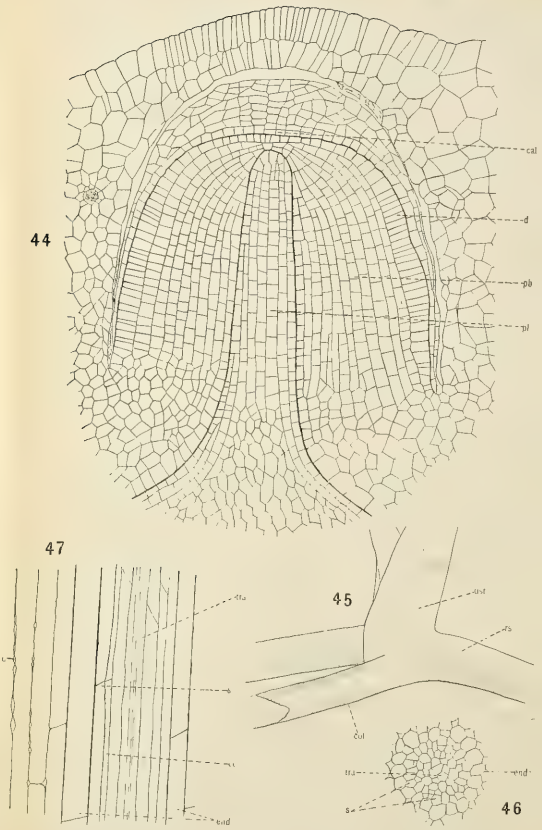


PLATE IX

Figure **48**.—Surface view of cells from epidermis of root, showing root hairs developing from the trichoblasts. × 210.

Figure **49**.—Rhachis with the two flowers; showing arrangement in the adult condition. × 12.

Figure **50**.—Rhachis and young flowers; showing arrangement in young stage. × 30.

Figure **51**.—Longitudinal section through nearly mature rhachis and flowers. × 20.

Figure **52**.—Very young floral primordia. Stippled portions represent regions which will develop the flowers. × 210.

Figure **53**.—Slightly older floral primordia. Stippled portions represent regions which will develop the flowers. × 210.

Figure **54**.—Older floral primordia. Floral scale leaf appearing. × 210.

Figures **55** and **56**.—Successively older stages in floral development. In figure 56 the primordia of pistils and stamens appear well defined. × 60.

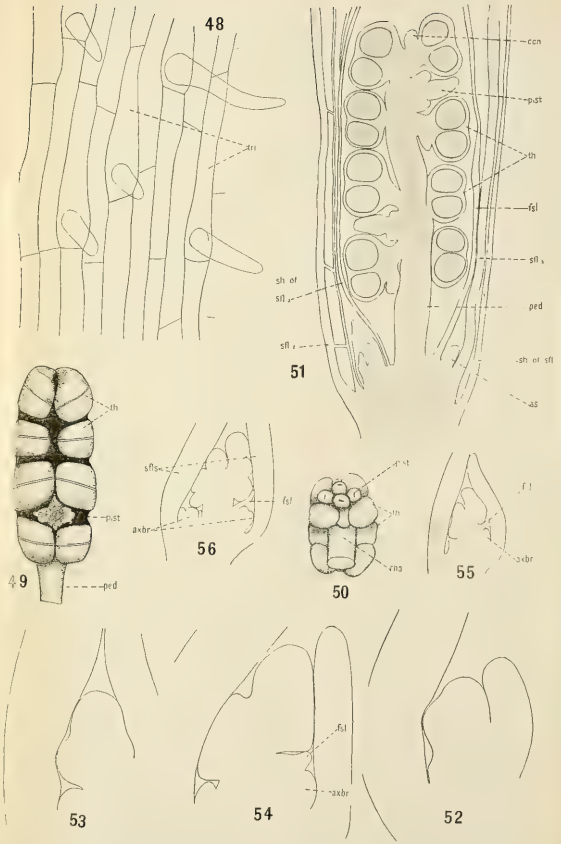


PLATE X

Figure 57, a and b.—Two views of a mature theca, the dotted triangular region representing the region of attachment to the connective. × 30.

Figures 58-66.—Median longitudinal sections illustrating development of the pistils.

Figure 58.—Section through flower rudiment; showing primordia of two pistils, an anther-connective at each side. × 75.

Figure 59.—Section of older stage; showing the beginning of the development of the stylar canal. × 75.

Figure 60.—Older stage. × 75.

Figure 61.—Older stage. One-sided development of the pistils commences. × 75.

Figures 62 and **63.**—Stigma commences to form. Stylar canal well developed. × 75.

Figure 64.—Stigma assumes peltate form. Ovule and embryo-sac well developed. × 75.

Figures 65 and **66.**—Development to approximately the mature form of pistil; showing the gradual oblique orientation of ovule. Figure 65, × 75; figure 66, × 37.

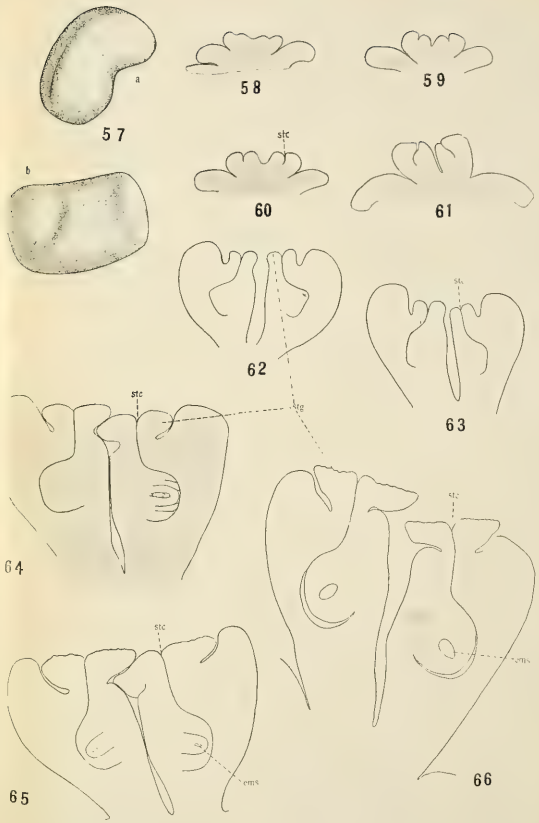


PLATE XI

Figure 67.—Cross section through young theca of a flower 0.2 mm. long, the measurement being taken in the direction of the dotted line shown in figure 68. Stippled cells represent the archesporial initials. × 600.

Figure 68.—Section of young flowers from which figure 67 is drawn, the actual length of each flower being about 0.2 mm. x marks the region represented in figure 67. Dotted line shows direction for measurement of the length of the flower. × 60.

Figure 69.—Cross section through slightly older theca of a flower 0.25 mm. long; showing division initiating development of septum, and also formation of the primary parietal layer. × 600.

Figure 70.—Section of flowers from which figure 69 is taken. x marks the region in figure 69. × 60.

Figure 71.—Cross section through theca of flower measuring about 0.3 mm. in length; showing sporogenous cells in the two sacs of the theca, two parietal layers, in places, and septum. × 600.

Figure 72.—Section of flowers from which figure 71 is taken. x marks the region shown in figure 71. × 60.

Figure 73.—Cross section through theca of a flower measuring 0.33 mm. in length; showing sporogenous cells in two sacs of theca, two parietal layers, and septum. × 400.

Figure 74.—Cross section through one of the sacs of a theca of a flower measuring about 0.5 mm. in length. Parietal layers often three in number. × 400.

Figure 75.—Group of cells from cross section of pollen-sac; showing pollen mother-cells surrounded by the still intact tapetum. × 600.

Figure 76.—Portion of section through older pollen-sac; showing pollen mother-cells and dissolution of tapetal cells. × 600.

Figure 77.—Section of megasporangium showing two megaspore mother-cells and one parietal layer. × 375.

Figure 78.—Section of megasporangium showing four daughter-cells resulting from a double mother-cell, and also two parietal layers. × 400.

Figure 79.—Section of megasporangium; showing the four potential megaspores, the wall separating the two upper ones being approximately parallel to the plane of the paper. The three upper cells are all being resorbed. × 375.

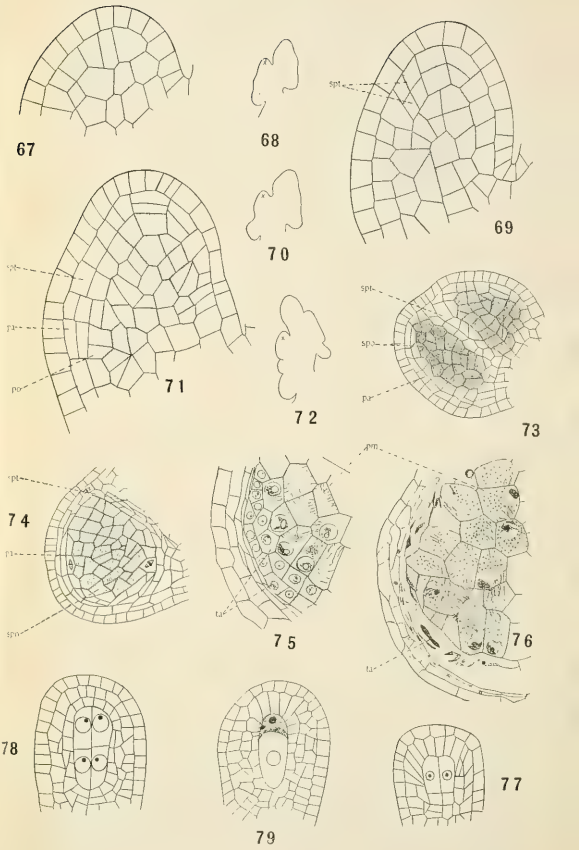


PLATE XII

Figure 80.—Section of megaspore mother-cell with surrounding cells, showing spindle of first reduction-division. Eight chromosomes were counted in this spindle, four of which are shown in the figure. × 800.

Figure 81.—Portion of section of megasporangium, showing the unusual condition of the four potential megaspores in a row, the two upper already being resorbed. Or, judging from the very indistinct wall separating the two lower cells and from their size, this may be a case where only three megaspores were formed, and the lowest has undergone the first division. × 800.

Figure 82.—Portion of section of megasporangium, showing omission of formation of wall between the two outer potential megaspores, these and the next lower becoming resorbed. × 800.

Figure 83.—Portion of section of megasporangium showing young embryo-sac with two nuclei; upper potential megaspores and part of surrounding tissue becoming resorbed. × 800.

Figure 84.—Young embryo-sac with four nuclei; showing also remnant of upper potential megaspores. × 800.

Figure 85.—Mature embryo-sac, showing synergidae, upper polar nucleus, egg, lower polar nucleus, and antipodals. × 800.

Figure 86.—The three antipodal cells lying in pouch at base of nature embryo-sac. × 800.

Figure 87.—Pollen mother-cell, synapsis stage. × 800.

Figure 88.—Young pollen-grain in tetrad before the dissolution of the tetrad wall. × 800.

Figure 89.—Pollen-grain just before formation of generative cell, showing enclosed starch grains and beginning of wall thickenings. × 800.

Figure 90.—Pollen-grain showing spindle preparatory to formation of generative cell. × 800.

Figure 91.—Cross section through middle of pollen-grain at stage shown in figure 90. × 800.

Figure 92.—Pollen-grain just after formation of generative cell. × 800.

Figure 93.—Longitudinal section through almost mature pollen-grain, showing tube-nucleus and generative cell just previous to formation of male cells. × 400.

Figure 94.—Longitudinal section of mature pollen-grain showing the two male cells still united, and the degenerating tube-nucleus. × 375.

Figure 95.—Longitudinal section of mature pollen-grain, showing characteristic dumbbell shape. × 175.

Figure 96, a and b.—Surface and profile views, respectively, of the pollen-grain wall thickenings, at mature stage. × 800.

Figure 97.—Pollen-grains, during the dissolution of the tetrad walls and formation of the pollen-grain wall. × 800.

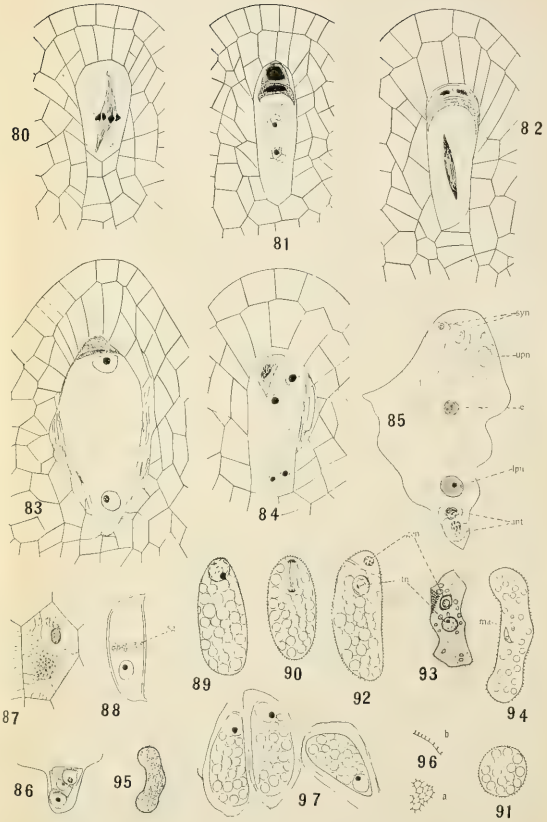


PLATE XIII

Figure 98.—Three-celled proembryo of *Ruppia rostellata*, showing basal suspensor-cell and two smaller embryo-cells. After Murbeck. × 446.

Figure 99.—Nine-celled embryo of *Ruppia rostellata*, showing basal suspensor-cell and eight small embryo-cells. After Wille. × 340.

Figure 100.—Thirteen-celled embryo, showing division into three transverse segments of four cells each, and a large suspensor-cell with nucleus and cytoplasm in the characteristic position. × 800.

Figure 101.—Longitudinal section through older embryo, the heavy lines marking the outlines of the cells shown in figure 100. × 800.

Figure 102.—Longitudinal section of older embryo, showing the outlines of the original segments and the beginning of the formation of dermatogen, at least in the terminal segment, at left. × 800.

Figure 103.—Longitudinal section of embryo with a diameter of about 0.05 mm.; showing rather irregular segment lines, and globular form of embryo. × 800.

Figure 104.—Longitudinal section of embryo of a diameter of about 0.075 mm.; showing increase in size of all cells, but only a slightly greater number than in figure 103. × 800.

Figure 105.—Longitudinal section of embryo measuring about 0.085 mm. in length; showing commencement of elongation, and divisions in the terminal segment, at the left, indicating approach of cotyledonary development. × 300.

Figure 106.—Longitudinal section of embryo measuring about 0.135 mm. in length; segment limits obscure; apparently the terminal segment is commencing the formation of stem as well as cotyledon. Basal portion shows cells which go to form the rudimentary primary root. × 375.

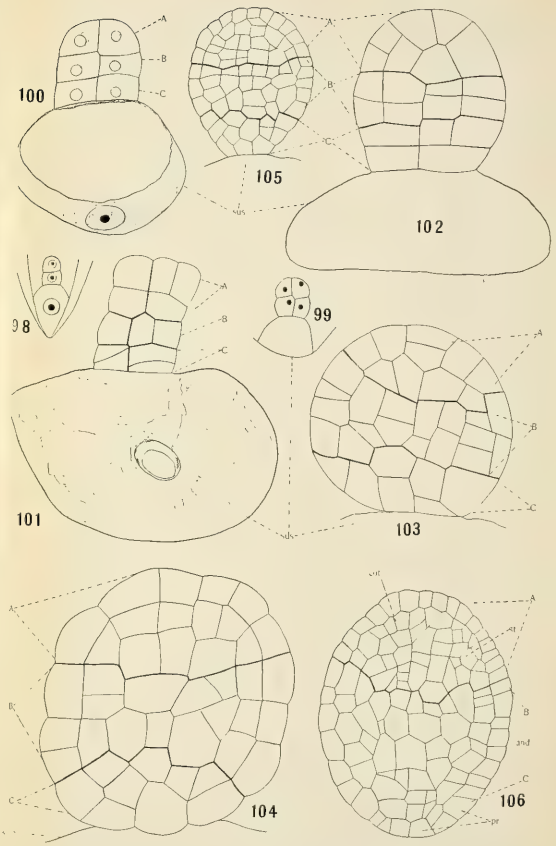


PLATE XIV

Figure 107.—Part of longitudinal section through older embryo, showing origins of cotyledon and stem apex. × 375.

Figure 108.—Section of embryo from which figure 107 is taken. x marks the region figured. × 75.

Figure 109.—Longitudinal section of embryo measuring about 0.35 mm. in length; showing development of cotyledon and stem-apex or epicotyl. × 50.

Figure 110.—Basal region of embryo shown in previous figure, illustrating the group of cells which forms the rudimentary primary root. × 300.

Figure 111.—Single storage cell from hypocotyl of embryo shown in figure 109, showing enclosed starch grains. × 600.

Figure 112.—Upper part of longitudinal section of nearly mature embryo shown in figure 113; showing stem-apex with growing-point and second leaf rudiment, part of cotyledon with section of basal sheath, and adventitious root. × 212.

Figure 113.—Longitudinal section of nearly mature embryo from which figure 112 is drawn; showing hypocotyl, epicotyl, cotyledon, and adventitious root. × 35.

Figure 114.—One of storage-cells from hypocotyl of embryo shown in figure 113. × 600.

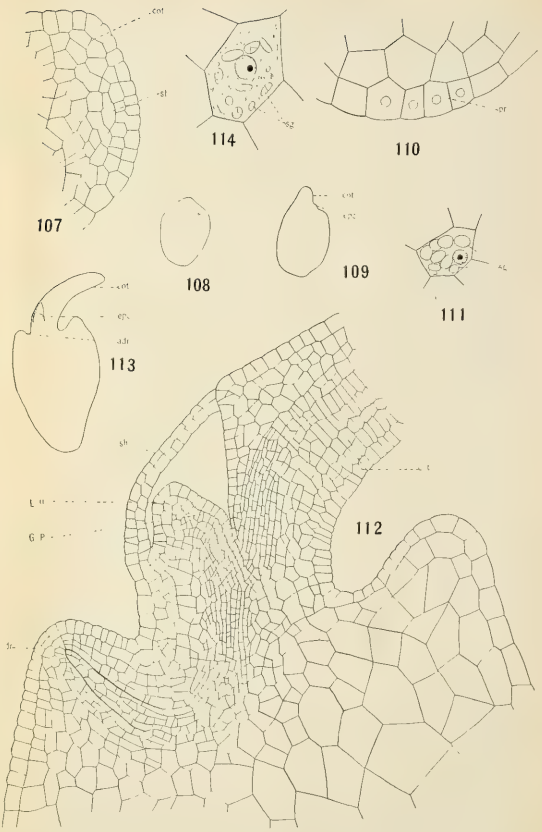


PLATE XV

Figure 115.—One of the storage cells from hypocotyl of embryo represented in figure 116, showing increased size of all parts. × 800.

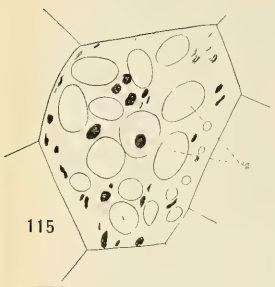
Figure 116.—Nearly mature embryo, older than that shown in figure 113, and showing the parts represented in the latter. × 35.

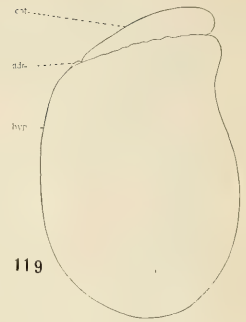
Figures 117 and **118.**—Two views of a cotyledon, dissected from a mature embryo, showing position of epicotyl and the overlying cotyledonary sheaths. Figure 118, represents the narrow cleft between the sheaths. × 35.

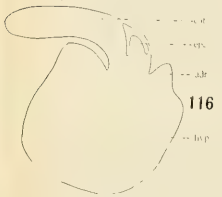
Figure 119.—Mature embryo dissected from ripe seed. × 35.

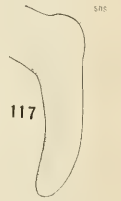
Figure 120.—Seedling about three days old; showing cotyledon and young stem with the first node, adventitious root with root hairs, and the thick, storage part of the hypocotyl still within the hard shell. × 6.

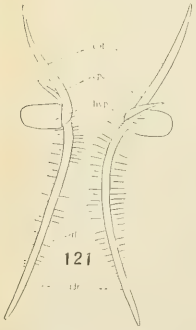
Figure 121.—Two views of young seedling; showing long adventitious root with root hairs, cotyledon, epicotyl, &c. The hard shell has been purposely removed from the hypocotyl. × 6.











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